THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

THE FLORA OF THE KANSAS FLINT HILLS

By

William T. Barker

Vol. XLVIII Pages 525-584 October 17, 1969 No. 14

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The Flora of the Kansas Flint Hills

William T. Barker[1]

ABSTRACT

This paper reports 987 species of vascular plants for the Kansas Flint Hills. Descriptions of the topography, drainage, climate, original vegetation, disturbance of the original vegetation and the present vegetation of the region are included.

The Kansas Flint Hills area is a region of transition where eastern distributed and western distributed species meet. Approximately 25% of the native species that occur in the Kansas Flint Hills reach either their western or eastern limit of distribution in Kansas within the Hills. In addition to those species that reach their limit of distribution within the Flint Hills region, there are 100 species that are limited in their westward or eastward distribution in Kansas by the Flint Hills but do not occur in the Hills.

INTRODUCTION

The Flint Hills, as they are commonly called due to the cherty nature of the soil, are a range of hills which cross Kansas in a north-south direction and extend into Oklahoma. On the map these hills appear as a somewhat elongated oval-shaped area about 200 miles from tip to tip, being some 50 miles or somewhat more than two counties in width (Map I).

No consistency in designating the area is found, either in professional or in popular literature. Various names such as Kansas Mountains, Permian Mountains, Flint Hill Pastures, Flint Hill Uplands, Bluestem Pastures and Flint Hills-Bluestem Pastures have been used in referring to the area. As pointed out in Kollmorgen and Simonett's (1955) comprehensive survey of the bluestem grazing operations in Chase County, the precise boundaries of the Flint Hills have not been defined to everyone's satisfaction. The name Flint Hills apparently implies different things to different people. To the geologist, the Flint Hills constitute an area where certain bedrock, notably

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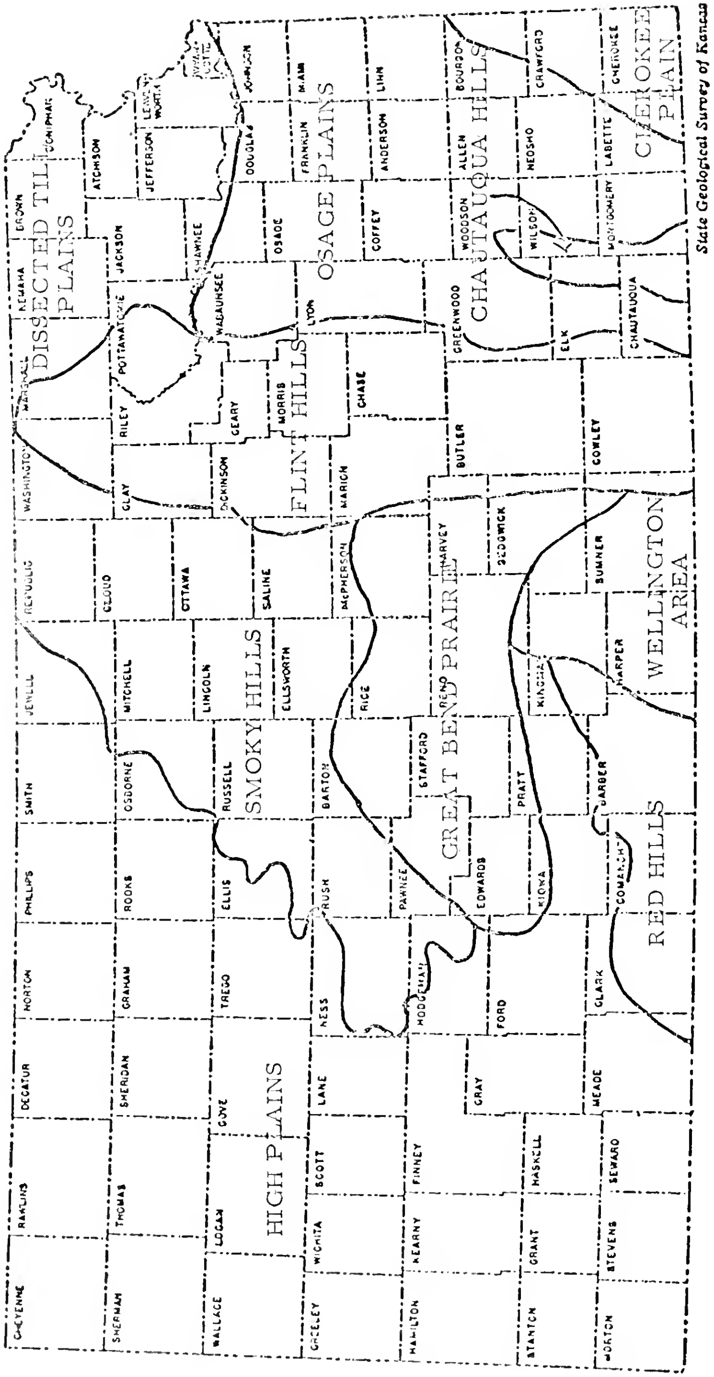


State Geological Survey of Kansas

Map I. Physiographic Map of Kansas (As modified from Schoewe, 1949) cherty limestones, outcrop. Kollmorgen and Simonett (1955) point out that Jewett (1941) and Schoewe (1949) do not agree on the extent of the Flint Hills. To the botanist and the range scientist, the Flint Hills constitute an area of natural vegetation whose substrate only incidentally contains chert rock (McGregor, 1955, and Bidwell, 1966). To the northwest of the Flint Hills one encounters the Dakota Sandstone Formation which is covered with a tall grass vegetation with the same dominant bluestems as found in the Flint Hills. The same is true to the east, where much of the Osage Plains is covered by tall grass vegetation with the same dominant bluestems. The area designated as the Flint Hills is by no means coterminous with big pasture country in Kansas. To the zoologist, the Flint Hills are a natural habitat for certain animal species and a barrier to the westward distribution of eastern species and to the eastward distribution of western species (Gier, 1967). To the native Kansan, they constitute an unusual bluestem mantled landscape whose steep rocky slopes and accordant summits create a panoramic beauty that constantly changes with the seasons. For this study, a broad interpretation of the Flint Hills was followed. It includes not only the outcrops of the Florence, Schroyer and Three-Mile cherty limestone strata, but also the adjacent shallow soils on massive limestone cuestas, the associated steep slopes and the areas of deep, nearly level, clayey soils of the broad ridges. With this interpretation, the Flint Hills include parts of the following counties: Cowley, Butler, Chase, Marion, Lyon, Morris, Geary, Wabaunsee, Riley, Pottawatomie and Marshall. The total area studied includes approximately 4.5 million acres.

This study of the vascular flora of the Kansas Flint Hills was made with two objectives in mind. The first was to compile a list of the vascular plants for the area and to support this list with specimens filed in the Herbarium at the University of Kansas. The second objective was to study the individual species in the environment in which they grow and to record this information.

Other workers have compiled and in some cases published lists of vascular plants from portions of the area. Carruth (1877) listed 52 species from the area. Most of these were from the vicinity of Irving, a small town in Marshall County. Hitchcock (1899) recorded some 600 species for the Kansas Flint Hills. Stevens (1917) lists plants he collected from the Manhattan (Riley County) and Blue Rapids (Marshall County) area which included 600 species. Maus (1919) lists 495 flowering plants for Wabaunsee County. Gates (1940) listed 602 taxa for the Kansas Flint Hills. Fish (unpublished thesis, 1953) listed 813 species for Riley County, 693 species for Pottawatomie County and 528 species for Wabaunsee County. There are other papers which list species for the area but none of these studies involved systematic inventories (Aldous, 1934; Anderson, 1951, 1953, 1965; Anderson & Fly, 1955; Weaver, 1954). From this review of the literature, it is evident that a complete study of the vascular flora of the Kansas Flint Hills had not been done. Since this area is economically important as a grazing area and is a region of transition where eastern distributed and western distributed species meet, it was felt that a floristic study of the Kansas Flint Hills would be a worthwhile addition to the knowledge of Kansas plants.

Prior to this study extensive fieldwork had been done in the area by Dr. R. L. McGregor and Mr. Steve Stephens of the Department of Botany, University of Kansas. As a result, many plant specimens deposited in the University of Kansas Herbarium have supplemented the writer's collections.

ACKNOWLEDGMENTS

The writer is indebted to Dr. R. L. McGregor for first suggesting the problem studied, for many suggestions and criticisms, and for arranging financial assistance for the necessary fieldwork. Special thanks are due to Drs. McGregor, Baxter and Thompson, of the University of Kansas Botany Department, for their allotment of time in editing of this paper. An acknowledgment is also due Mr. Steve Stephens, of the University of Kansas Botany Department, whose aid in collecting has contributed greatly to this study.

TOPOGRAPHY

In terms of major physical divisions of the United States, Kansas lies almost wholly within the Interior Plains (Fenneman, 1939). The Interior Plains Division is comprised of two provinces in Kansas and both of these extend far beyond the borders of the State. These are the Central Lowland, including roughly the eastern third of Kansas, and the Great Plains, to which the remaining two-thirds of Kansas belongs. The Kansas Flint Hills are a part of the Central Lowland. The Central Lowland has the following units in Kansas: Dissected Till Plains, Osage Plains, Chautauqua Hills and the Flint Hills (Map I).

In general, the Flint Hills, as well as the Osage Plains, consist of a series of escarpments between which are flat to gently rolling plains. The escarpments are east-facing and tend irregularly from southwest to northeast. The underlying strata are made up of unequally resistant alternating hard and soft Pennsylvanian formations of limestones and shales which are gently inclined to the west and northwest. Due to differential erosion in these alternating hard limestones and soft shales, the series of cuestas have developed in the area. In the Flint Hills these Pennsylvanian deposits are capped by Permian strata and erosion of these strata accounts for the cherty nature of the soil.

The surface of Kansas gradually slopes downward from the western border eastward, at a rate of 10 to 15 feet per mile. Along the western edge of the Flint Hills the topographic relief is almost imperceptible. By contrast, it is the highly dissected east-facing escarpment with its terraced slopes that makes possible the separation of the Flint Hills from the lower or east division of the Osage Plains (Schoewe, 1949). This eastern border of the Flint Hills is probably the most rugged surface feature in Kansas. The eastward-facing escarpment is not everywhere one great step but is more commonly made up of two or three closely spaced rock benches, with the intervening slopes rising with steep gradients to the highest bench which everywhere forms the broad upland of the Flint Hills. The relief of this east-facing escarpment ranges from 300 to 350 feet. The surface of the uplands slopes gently toward the Arkansas River Valley. There are places where the uplands are pitted by sink holes. The uplands generally range between 1,500 and 1,600 feet above sea level. The streams in the Flint Hills have deep precipitous channels lined with outcropping rock ledges. In places, where these have cut into limestones, narrow box-like channels have been produced, but where they have cut into the less resistant shales, the valleys immediately open out and the valley slopes are much gentler. A relief of 300 to 350 feet is often encountered from the stream valley floor to the uplands. In Cowley County, Grouse Creek (unlabeled stream, Map II), a south-flowing left-handed tributary of the Arkansas River, divides the Flint Hills into two ridges, the easternmost one of which is known as the Big Flint Hills, and the western one as the Little Flint Hills (Adams, 1903). North of the Kansas River, the Flint Hills diminish in height and become a less conspicuous topographic feature. This northern part of the Flint Hills has been glaciated, as evidenced by scattered erratics and till deposits, and is included in the Attenuated Drift Border unit of the Dissected Tills Plains section (Schoewe, 1949).

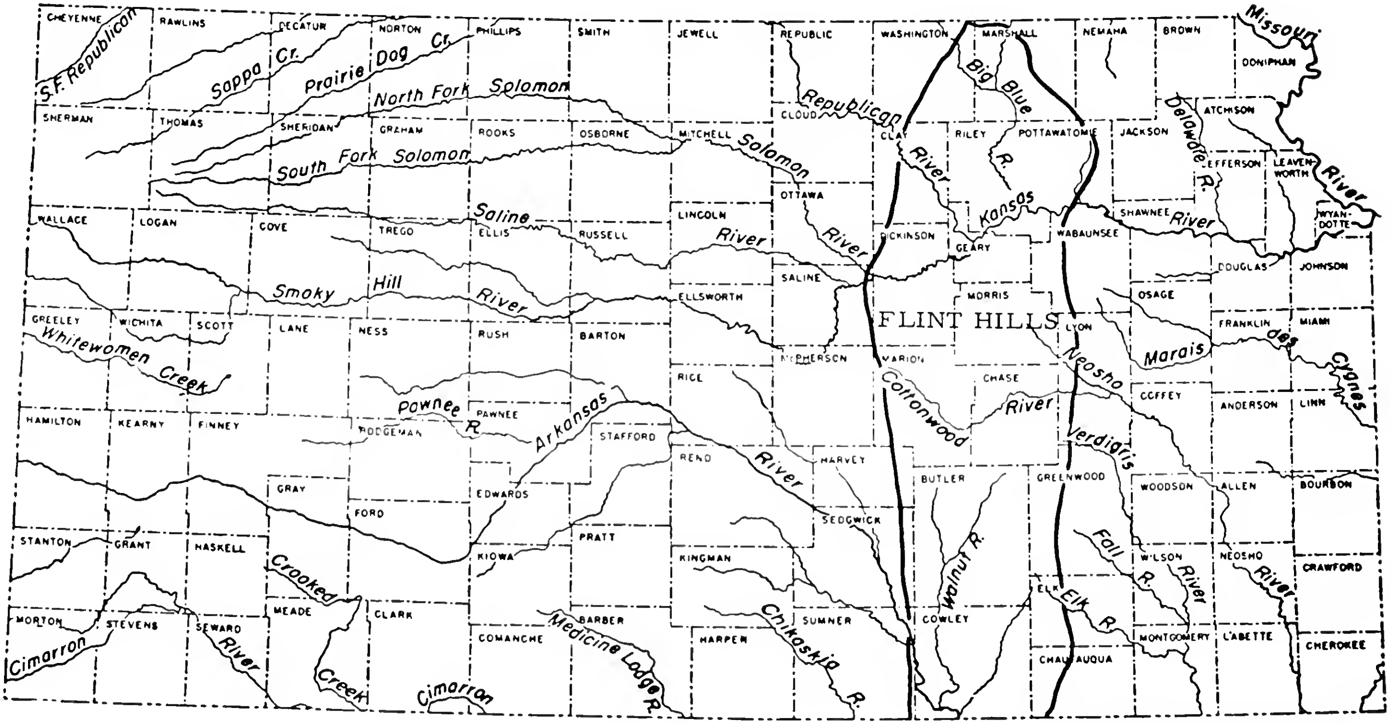
DRAINAGE

The only river to cut through the Flint Hills upland from west to east is the Kansas River (Map II). The Kansas River flows in a well-defined, rock-walled, terraced valley from two to three miles wide and from 150 to 200 feet deep. The northern part of the Flint Hills is drained by the Kansas River and its tributaries. Further south, numerous spring fed creeks give rise to several permanent rivers that drain the southern part of the Flint Hills. The Marais des Cygnes courses generally eastward roughly paralleling the Kansas River to join the Missouri River in Missouri. The Neosho and its principal affluent, the Cottonwood, head in the Flint Hills and flow southeast to join the Arkansas River in eastern Oklahoma. Paralleling the Neosho to the west is the Verdigris, with the Elk and Fall Rivers as its main tributaries. It unites with the Arkansas a few hundred feet above the Neosho in Oklahoma. The Walnut River rises on the west, or back slope of the Flint Hills and empties into the Arkansas a few miles above its point of exit from the state. Each of the rivers mentioned above have numerous tributaries which arise in the uplands. These are too numerous to mention here. All of these rivers and creeks run in wide, flat-floored valleys with high bordering bluffs and terraces. The valleys are subject to major floods that often spread widely. The bottom land soils are typically heavy though fairly productive. Numerous impoundments are found along the drainage areas throughout the area.

CLIMATE

The climate of the Kansas Flint Hills is one of the area's most variable features. Sudden changes in temperature, wind and precipitation are common. Temperature extremes vary from −32°F. to +118°F. with the averages being rather moderate (Flora, 1948). From April to December the prevailing winds come from the south, whereas during January through March northerly winds prevail. The periods of heaviest rainfall come in the fall and the spring with the average annual precipitation ranging from 30 inches in the northern part of the area to 35 inches in the southern part. The average growing season is 189 days in the south as compared to 176 days in the north part of the area. The average relative humidity during January ranges from 60 to 70 percent, whereas during July it ranges from 45 to 50 percent. These data were obtained by averaging relative humidity readings taken daily at noon (Flora, 1948). Snowfall is moderate and snow seldom remains for long on the ground.

Küchler (1967) points out that the mean values of annual and monthly precipitation have been recorded for many decades but they conceal the most critical of all climatic features, the rainfall reliability. In any given season the rains may come early or late; they may be evenly distributed throughout the growing season or be bunched together in a few hard showers; it may rain amply or very little. The seasonal aspect of the flora is greatly influenced by the seasonal distribution of rainfall. It is evident from the recorded climatological data that periodic drouths are characteristic of the region's climate. During the recorded history of the state there have been seven periods of dry weather of exceptional note: 1859-1868, 1872-1875, 1892-1894, 1901, 1915-1917, 1930-1940, and 1952-1956. Albertson and Tomanek (1965) have presented carefully documented observations of vegetational changes near Hays, Kansas, located in Ellis County, during 30 years which illustrate complex features of the ecosystems of the prairie. Unfortunately, there has not been a comparable study for the Kansas Flint Hills, but the effects of drouths in the area have not gone completely unnoticed. Hoyle (1938) stated that during the five year period, 1931-1936, one third of the maples and elms died due to dry weather. Gates (1945) stated that due to the dying out of prairie grasses during the drouth (1930's), *Gutierrezia dracunculoides* spread into the prairie lands at an amazing rate but by 1945, after the drouth had broken, the prairie grasses had again replaced the *Gutierrezia*. Agrelius (1945) also commented on the disappearance of *Gutierrezia dracunculoides* after the drouth broke, and mentioned that *Anemone caroliniana* and *Viola pedatifida* had also become scarce in the more mesic times.



State Geological Survey of Kansas

Map II. Major Stream Courses of Kansas

ORIGINAL VEGETATION

From geologic and paleontologic studies (Frye & Leonard, 1952, 1957) it seems clear that the grassy plains of Kansas are not a recent development. It is thought that the climatic control of the Kansas vegetation has been the same as it is today since Pleistocene times. Wedel (1959) feels that the grassland vegetation antedates man's demonstrable presence on the scene.

A knowledge of the vegetation of the Kansas Flint Hills before the time of settlement must be gained largely from notes of explorers, travelers and surveyors. These written records occasionally include mention of native plants. Malin (1967) points out that the explorers and travelers usually went west after the grass started in the spring, and, if they returned, usually did so in the late summer and fall, and that the reports on the vegetation of these seasons tended to develop into a stereotype for the grass country. It is evident as one reads the notes of these early people that they were tree conscious and the grasslands were unfamiliar and quite monotonous to them. Tree species are mentioned often in their notes but only occasionally are the herbaceous species mentioned.

The Flint Hills vegetation prior to the time of white settlement must have been similar to what one sees in the area today. While in Pottawatomie County, Fremont (1845) described the many tributaries of the Kansas River as looking like "trenches in the prairie usually well timbered."

Möllhausen (Taft, 1948) traveled from west to east across Kansas in 1858 and he relates how just west of Marion County the grass became more fresh and luxuriant than the short, insignificant, but nonetheless nourishing buffalo grass *(Buchloe dactyloides)*. At about the same time he relates how the depressions became deeper, the elevations higher, and the springs and brooks more numerous.

Möllhausen wrote on July 15, 1858, "We camped several miles east of Diamond Springs (undoubtedly within the Flint Hills region) on an unnamed brook. Tall grass surrounded us, with an annoyance which we could not avoid." It is interesting to note that in reference to the country between Council Grove and Kansas City, Möllhausen wrote, "I shall avoid describing the rest of the journey in diary form for on the entire route from the Neosho to the Missouri (Rivers) we were constantly in surroundings whose characters remained unchanged." If originally unbroken prairie extended all the way from Kansas City through the Flint Hills region, as Möllhausen's statement indicates, it is not surprising that the early people did not describe the Flint Hills in more detail. Undoubtedly, the region is a more prominent region in the landscape now than it was in 1858.

Early observations of the vegetation in the southern part of the Flint Hills were recorded by members of a surveying party that surveyed the southern boundary line of Kansas in 1857 (Caldwell, 1937; Miller, 1931). These people also indicate that the stream valleys were well-timbered and that the hillsides and uplands were covered with tall grasses of a high quality.

The Kansas Flint Hills counties were surveyed during the year 1856-1871. The original surveyor's notes, taken in the field during the surveys of township and section lines, contain a general description of the land and often observations of the vegetation. These original notes are on file at the State Auditor's Office in the State House in Topeka, Kansas. It is evident from these notes that the surveyors were tree conscious and were mainly interested in land suited for farming and therefore were usually very unimpressed with the vast areas of rolling prairie. As one reads these notes he is impressed by the uniformity of observations of the landscape. The ravines, creeks, streams and rivers are described as being "well timbered," while the slopes and uplands are described as being covered with "prairie or grassland." Frequent mention was made of the following trees: elm, oak, burr oak, hickory, cottonwood, walnut, hackberry, sycamore, redbud, willow, hazel, box elder, ash, cedar, linden, dogwood, plum and prickly ash. This list of trees compiled from the historical records corresponds rather well with the list of the common trees of the present woodlands.

These first observations, prior to or at the beginning of white settlement in the region, indicate that most of the uplands and hillsides were covered by tall grass prairie vegetation and that the creeks, streams and rivers were lined with trees.

SETTLEMENT AND DISTURBANCE OF THE ORIGINAL VEGETATION

Disturbances of the original vegetation by the plow, ax and grazing accompanied white settlement of the area and have increased and continued to the present day. The first major steps in which occupation were initiated in the early 1840's when missions were established at Council Grove (Morris County) and St. Mary's (Pottawatomie County) to teach general farming and cattle grazing to the Pottawatomie Indians (Malin, 1942). During the next several years, more small farmers settled in the Big Blue, Kansas, Neosho and Cottonwood river valleys. These first settlers, being farmers, were mainly interested in the bottom lands and were of the opinion that the uplands were unproductive. Timber was cut from the bottom lands to build houses and other improvements and to clear fields in preparation for general farming. After the Civil War, many more small farmers came to settle, first in the bottom lands and finally in some of the uplands. Much of the native grassland was plowed and more timber was cut from the river valleys.

During the decade of the 1870's, the agricultural interests of the region were relatively diversified. There were at least four types of activities represented in the area: general farming, which emphasized grain crops; farming, which emphasized the raising of corn; the breeding of fine stock; and the maturing and grazing of transient cattle (Malin, 1942).

During the years 1872-1875 there was a severe drouth. By 1879 many of the upland farms had been abandoned and the former cultivated fields allowed to go back to native grass. At this time, the uplands were generally used for grazing and the bottom lands were used for general farming.

During the decade of the 1880's the region experienced a livestock boom (Malin, 1942). The use of barbed wire began slowly about 1879 and 1880 and reached boom proportions by 1883. The bottom lands were fenced from the uplands first and by 1885 the uplands had been fenced off into separate pastures. This in a sense brought about a sharp line of distinction between the small farmers in the bottom lands and the cattlemen controlling the uplands that exists even today (Kollmorgen & Simonett, 1965).

In the first part of the 1880's the major emphasis was placed upon the expansion and improvement of local cow herds, but by the latter part of the decade this practice was replaced by the maturing and grazing of transient cattle. By 1886 cattlemen realized that cattle could be fattened to market weights on the Kansas Flint Hill prairies in a single summer. The practice of bringing yearling steers to the area by rail in mid-April, allowing them to graze on the bluestem prairies through the summer months, and then shipping them by rail to eastern markets by mid-August or, at the latest, mid-September soon became the common rule. Much outside capital was invested by southwestern cattlemen and various syndicates organized during the 1880's to assemble acreages large enough for these extensive cattle operations. To build large enough acreages required large sums of capital and the small farmers were never able to compete with the cattlemen in acquiring the uplands. So, early in the history of the area, absentee ownership of the uplands was established. Today, more so than ever before, the uplands are controlled by absentee owners who are mainly interested in stock raising rather than general farming. For an example, in 1959 in Chase County, only 45% of the land was locally owned. It is also interesting to note that only 30% of all the pasture land was locally owned while 81% of the cropland was locally owned (Kollmorgen & Simonett, 1965).

Due to changes in agricultural technology and economic conditions in the United States, the number of small farmers in the region has steadily declined and the large holdings of the cattlemen have continued to increase in size at the expense of the small farmers and small ranchers. In recent years the practice of maturing and grazing of transient cattle has given way somewhat to the practice of maintaining local cow herds. This practice increases grazing pressures on the prairies. The native grasses of the region begin to grow in March and continue their development until the first killing frost in early October. Transient cattle have usually been turned into the prairies by mid-

April and are then shipped to market around mid-August or by mid-September at the latest. Anderson (1953) feels that the maintenance or relatively good native prairie in the region has been due to the fact that since the cattlemen have wanted rapid gains on their steers, light stocking has been practiced. Early in the history of the area large holdings were built and these owners could afford the luxury of light stocking. Along with this, cattle often reached market condition by mid-summer and were removed, thus allowing the native grasses to recover by allowing carbohydrate reserves to accumulate, flowering, seed set and finally, reseeding of the prairie.

Overgrazing in the Flint Hill region has occurred often, especially where both farming and stock raising has been practiced and the smaller ranges have been more or less continually overstocked. Weaver (1954) stated that light grazing involves only a shift in number of plants, not in species composition of the native prairie. Heavier overgrazing practically eliminates the big bluestem, while little bluestem, sideoats grama, tall dropseed and buffalo grass increase. If the overgrazing becomes more severe, there is an invasion of weeds and many brushy species. In the northern part of the Flint Hills, *Juniperus virginiana* is becoming a serious problem in overgrazed situations. Throughout the area the brushy species, *Cornus drummondii, Rhus aromatica* and *Rhus glabra* increase during overgrazing. Ranchers are using selective herbicides, 2,4-D (2, 4-D Dichlorophenoxyacetic acid) and 2, 4, 5-T (2, 4, 5-Trichlorophenoxyacetic acid), to control these. These selective herbicides kill many dicotyledonous forbs, especially the leguminous plants, which are important prairie components.

A trend that is becoming more and more evident is that cow herds are now being maintained in the Flint Hill region. This practice increases the grazing pressures on the prairies since the cows and calves are on the prairies nine to twelve months rather than just in the summer months, as with the transient steers. To emphasize this point, a common rule-of-thumb that ranchers follow in stocking their pastures holds that a good to superior pasture should carry a long-yearling or two-year old steer on five acres of pasture for a six month summer grazing period whereas, a cow or a cow with a small calf requires at least twelve acres for a nine-month grazing period.

Burning of the prairies in the spring has long been a common practice. Many ranchers feel that if they burn early each spring they will have better grass sooner, and others burn in an attempt to control brush. Anderson (1965) points out that the burning of bluestem range in the Flint Hill region reduces soil moisture. Burning of prairies in very dry years undoubtedly causes deterioration of the condition of native prairie. Anderson (1965) suggests the following rules for ranchers in the region: "Burn no more than is necessary for good range management and good livestock husbandry. If burning is practiced, do it in late spring rather than earlier, recognizing that soil moisture levels, and hence herbage yield, will be reduced by burning. The earlier one burns, the less herbage he will have for harvest by livestock."

"Improvements" that man has made and is making in the area, such as building roads and impoundments, will have an influence on the flora of the area. Many acres of native vegetation are destroyed when a new road or impoundment is built. Disturbances of this sort provide open habitats and the number of plants of the weedy species of the area will increase. The number of aquatic plants will increase in the new aquatic habitats produced. A few new species may become established in these new habitats.

PRESENT VEGETATION

The largest remaining tract of true prairie in Kansas occupies the Flint Hill region. As previously stated, the region includes approximately 4.5 million acres. According to the 1965 Biennial Report of the Kansas State Board of Agriculture there are about 3 million acres of pasture (prairie) and approximately 1.5 million acres of cropland and woodland in the Flint Hill counties. In 1965 171,000 acres of native prairie was mowed for hay.

The vegetation of the Flint Hills region has been subjected to disturbances of various sorts throughout its history. Various degrees of degradation from the natural state can be found due to these disturbances and it is beyond the scope of this paper to discuss all of these. The habitats available for plant life in the Flint Hills are well-defined topographically and are easily recognized by their characteristic vegetation. These habitats range from aquatic situations provided by streams and artificial impoundments to the more xeric upland prairie. The following habitats are typical of the Kansas Flint Hills.

SEEPAGE AREAS, STREAMS AND ARTIFICIAL IMPOUNDMENTS

In the Flint Hill region aquatic plants are found in seepage areas around springs, in and along streams and artificial impoundments. In relatively deep water of impoundments and slow-moving streams there may be several species of submerged aquatics. Examples of these are *Ceratophyllum demersum, Myriophyllum heterophyllum, M. pinnatum, Potamogeton diversifolius, P. obtusifolius* and *P. pectinatus.* Nearer the shores in shallow water there are plants which are rooted in the mud and whose leaves float on the water. Some of these plants are *Bacopa rotundifolia, Jussiaea repens* and *Nuphar advena.* Among these plants are found free-floating plants such as *Lemna minor, L. perpusilla, Spirodela polyrhiza* and *Wolffia columbiana.* There are many plants, rooted below the water at the edge of these aquatic situations, with their foliage above the water. These include *Alisma triviale, Echinodorus cordifolius, Eleocharis calva, E. compressa, E. macrostachya, E. obtusa, Heteranthera dubia, H. limosa, H. reniformis, Juncus diffusissimus, J. interior, J. torreyi, Sagittaria latifolia, S. montevidensis, Scirpus validus, Spar-*

ganium eurycarpum and *Typha latifolia.* In the moist soil found along the margins of these aquatic situations, the vegetation usually consists of smart weeds, grasses, sedges and occasional shrubs. Examples of these are *Polygonum bicorne, P. lapathifolium, P. pennsylvanicum, P. punctatum, Rumex altissimus, R. crispus, Echinochloa crusgalli, Eragrostis hypnoides, Glyceria striata, Leersia oryzoides, L. virginica, Leptochloa fascicularis, Phragmites communis, Carex crawei, C. crus-corvi, C. emoryi, C. frankii, C. hyalinolepsis, C. hystricina, C. normalis, C. vulpinoidea, Cyperus erythrorhizos, C. esculentus, C. ferruginescens, C. strigosus, Scirpus atrovirens, S. lineatus, Amorpha fruticosa, Cephalanthus occidentalis, Salix caroliniana, S. interior* and *S. nigra.* Outside of the latter zone of vegetation there is an abrupt change to the surrounding plant community, whether it is a prairie or a woodland community.

In seepage areas below springs, such plants as *Equisetum laevigatum, Spartina pectinata, Typha latifolia, Carex annectans, C. crawei, C. interior, C. lanuginosa, C. vulpinoidea, Cyperus ferruginescens, C. strigosus, Eleocharis obtusa, E. calva, E. compressa, E. macrostachya, Furiena simplex, Scirpus atrovirens, S. lineatus, Juncus torreyi, Nasturtium officinale, Prunella vulgaris, Veronica angallis-aquatica, Bidens frondosa, B. polylepis, B. cernua* and *B. vulgata* are found. Just a few feet away from the seepage area very dry conditions are usually found and a typical prairie community usually exists.

Woodland

In the Kansas Flint Hills limited amounts of woodland are developed along floodplains, ravines and steep hillsides. In the Flint Hills region one finds the greatest proportion of woodlands in the northern counties and the lowest proportion in the southern counties. When one considers the major stream courses and the resulting erosional patterns of the region it becomes quite obvious that there are more habitats suitable for the development of woodlands in the northern and southern parts (see Map II). In the north, the Kansas River courses from west to east through the region. There are numerous large (Big Blue, Little Blue and Vermillion) rivers and small north-south tributaries of the Kansas River that dissect the area to the north. Each of these north-south tributaries have their smaller tributaries that run east and west. The result is more floodplains, ravines, and steep hillsides (hence, more woodlands) in the north as compared to the central and south portions of the area. The Cottonwood and Neosho Rivers are the only major streams in the central part of the Flint Hills. The floodplains of these streams are wooded and they have their small wooded tributaries. However, the central portion is less dissected by the stream courses and the resulting valleys are usually wide with gently sloping sides. In general, the terrain of the central portion is more rolling, which favors the development of a prairie community rather than a woodland community. In the southern part of the region the Walnut River and Grouse Creek dissect the area in a north-south direction and their tributaries dissect the area in an east to west fashion. The resulting erosional pattern provides suitable sites for the development of woodlands.

The floodplain woods, as would be expected, are more mesic than the woods encountered along the ravines and on the hillsides. *Ulmus americana* dominates the floodplain woods. Other important tree species found in these woods are *Ulmus rubra, Platanus occidentalis, Populus deltoides, Acer negundo, A. saccharinum, Fraxinus pennsylvanica* var. *subintegerrima, Celtis occidentalis, Salix amygdaloides, S. nigra, S. interior, Morus rubra,* and *Juglans nigra.* Common shrubs found in the understory of the floodplain woods are *Ribes missouriense, Sambucus canadensis, Asimina triloba* and *Euonymus atropurpureus.* Woody vines that are found in these woods include *Celastrus scandens, Parthenocissus quinquefolia, Rhus radicans, Smilax hispida, Vitis cinera, V. riparia* and *V. vulpina.*

The floodplain woods are subject to periodic flooding and this has a profound effect on the herbaceous flora. The herbaceous species found in these woods vary from year to year or from flood to flood. The herbaceous species appear as spring, summer and fall aspects. Spring plants include *Chaerophyllum procumbens, Dicentra cucullaria, Phlox divaricata* var. *laphamii, Viola papilionacea, Galium aparine, Ellisia nyctelea, Oxalis stricta, Parietaria pennsylvanica, Carex amphibola, C. blanda, C. davisii, C. molesta* and *Ruellia strepens.* Conspicuous summer species are *Geum canadensis, Oxalis dillenii, Laportea canadensis, Urtica dioica, Silene stellata, Thalictrum dasycarpum, Chenopodium hybridum* and *Scrophularia marilandica.* Fall plants include *Bidens bipinnata, Eupatorium rugosum, Polygonum virginianum, Muhlenbergia brachyphylla, M. mexicana, M. racemosa, M. schreberi, Sicyos angulatus, Verbesina alternifolia* and *Ambrosia trifida.* The floodplain woods are relatively uniform in their composition throughout the region.

Progressing from the floodplain woods up the steep hillsides and ravines, an abrupt change in the vegetation occurs and a more xeric type of woodland is encountered. At the base of the steep hillsides and ravines *Quercus macrocarpa* and *Carya cordiformis* are common. In the northern part of the Flint Hills *Quercus muehlenbergii* becomes the dominant plant further up on the hillsides. In the southern portion of the region, *Quercus muehlenbergii* is replaced by *Q. prinoides* as the dominant tree high on the hillsides and in the ravines. Other important tree species found in these drier woods are *Ulmus americana, Celtis occidentalis, Cercis canadensis, Ostrya virginiana, Maclura pomifera* and *Gleditisia triacanthos. Juniperus virginiana* is a common tree in this type of woodland in the northern part of the Flint Hills. Dense stands of this tree are found in the northern woodlands but only scattered trees are found in the central and southern portions of the Flint Hills. Common shrubs found in the understory of this dry type of woods are *Aesculus glabra, Sym-*

phoricarpos orbiculatus, Rhus aromatica, Cornus drummondii, Staphylea trifolia, Zanthoxylum americanum, Rubus allegheniensis, R. flagellaris, R. occidentalis and *R. ostryifolius. Corylus americana* and *Rhamnus lanceolata* are common shrubs in the northern portion of the Flint Hills but are not found in the southern portion. *Ptelea trifoliata, Bumelia lanuginosa* and *Sapindus drummondii* are found frequently in the southern hillside woodlands but are not found in the northern woodlands.

One of the major differences between the woodlands in the Flint Hill region as compared with those of the Dissected Till Plains, the Osage Plains, the Chautauqua Hills and the Cherokee Plain is the reduced number of herbaceous species present. Very often there is little or no herbaceous cover in the dry hillside woods of the Flint Hills. The herbaceous species of these woods can be listed as spring, summer and fall aspects. Spring plants include *Erythronium albidum, Galium aparine, Viola papilionacea, Carex aggregata, C. bicknellii, C. brevior, C. cephalophora, C. heliophila, Antennaria plantaginifolia, Ruellia strepens* and *Parietaria pennsylvanica.* Conspicuous summer species are *Galium circaezans, Sanicula canadensis, Desmodium glutinosum, Phyrma leptostachya, Oxalis dillenii, Silene stellata, Campanula americana, Geum canadensis* and *Elymus virginicus.* Common fall species are *Hackelia virginiana, Agastache nepetoides, Helianthus hirsutus, Eupatorium rugosum, Polygonum virginianum, Ambrosia trifida, Solidago nemoralis, S. ulmifolia, Verbena urticifolia, Verbesina alternifolia, Bidens bipinnata, Uniola latifolia* and *Aster drummondii.* In the Flint Hills region woodlands are seldom, if ever, developed on the uplands. As one ascends to the uplands, a prairie community is abruptly encountered.

A zone of shrubby vegetation is common along the limestone benches on the escarpments. The shrubs that make up this zone are *Rhus aromatica, Cornus drummondii* and *Rhus glabra.*

PRAIRIE

The prairies found in the lowlands along streams are dominated by *Andropogon gerardi,* while *Sorghastrum nutans* and *Panicum virgatum* are common. Scattered colonies of *Tripsacum dactyloides* may be present and *Spartina pectinata* is often dominant in very wet places. Leaving the lowland prairie and ascending the prairie hillsides, *Andropogon gerardi* is still the dominant grass, but *A. scoparius* and *Bouteloua curtipendula* increase in abundance. On the uplands *Andropogon scoparius* is the dominant and other important grasses found are *A. gerardi, Bouteloua curtipendula, Panicum virgatum, Sorghastrum nutans, Bouteloua hirsuta, Buchloe dactyloides* and *Sporobolus heterolepis.*

As a result of his studies of numerous Flint Hill prairies, Weaver (1954) gives the following average species composition figures for the area: *Andropogon gerardi* 38.9%, *A. scoparius* 34.4%, *Bouteloua curtipendula* 5.3%, *B.*

hirsuta 4.2%, *Sorghastrum nutans* 2.9%, *Panicum virgatum* 2.9%, *Buchloe dactyloides* 1.9%, *Sporobolus heterolepis* 1.7%, and various forbs 2.2%.

Light overgrazing of Flint Hill prairies reduces the abundance of the tall grasses, *Andropogon gerardi* and *A. scoparius,* while *Bouteloua curtipendula, B. hirsuta* and *Buchloe dactyloides* become more abundant. At this stage of degeneration the *Andropogon scoparius* and *Bouteloua curtipendula* are reduced to scattered bunches and *Buchloe dactyloides* becomes dominant. As overgrazing becomes severe, *Andropogon gerardi* is eliminated and *A. scoparius* is greatly reduced in abundance. In cases of severe overgrazing, soil erosion often results and the native vegetation is nearly destroyed. *Aristida oligantha* readily invades these exposed sites and appears as light areas in the vegetation.

A number of species give the prairie spring, summer and fall aspects. The most apparent plants in the spring and summer aspects are forbs, and it is important to remember that forbs account for less than 3% of the prairie community. Before the dominant native grasses have a chance to grow, much of the spring aspect becomes apparent due to the colorful flowering species involved. Important spring species are *Anemone caroliniana, Antennaria neglecta, Carex meadii, Nothoscordum bivale, Lomatium foeniculaceum, Nemastylis geminiflora, Senecio plattensis, Sisyrinchium campestre, Achillea millefolium, Zigadenus nuttallii, Baptisia leucophaea, Baptisia australis* var. *minor, Asclepias viridis, Cacalia tuberosa, Polytaenia nuttallii, Callirhoe alcaeoides, Erigeron strigosus, Erigeron annuus, Echinacea angustifolia* and *Ratibida columnifera.*

The summer aspect of the prairie is less striking than that of the spring because by this time grasses have undergone considerable growth. Common plants of the summer are *Schrankia uncinata, Psoralea tenuiflora, P. argophylla, Petalostemon purpureum, P. candidum, Linum sulcatum, Cassia fasciculata, Monarda fistulosa, Hedyotis nigricans, Ruellia humilis, Silphium laciniatum, Asclepias verticillata, Salvia azurea, Liatris aspera* and *Liatris mucronata.* In the fall the flowering of the dominant tall grass species, *Andropogon gerardi, A. scoparius, Sorghastrum nutans* and *Panicum virgatum* gives the prairie its aspect along with other conspicuous plants such as *Euphorbia marginata, Vernonia baldwinii, Solidago missouriensis, Eupatorium altissimum, Solidago altissima, Kuhnia eupatorioides, Solidago rigida, Helianthus laetiflorus, H. maximiliani, H. grosseserratus, H. salicifolius, Gutierrezia dracunculoides, Artemisia ludoviciana, Aster ericoides, A. oblongifolius* and *Solidago graminifolia.*

Along the limestone benches and the summits of the escarpments the soil is very cherty and shallow. The native grasses do not grow well in these marginal sites but certain shrubs and forbs do grow well and when these plants are in flower it is easy to observe these zones. In the spring, blooming

Amorpha canescens is common, followed in the summer by *Monarda fistulosa.* As *Monarda fistulosa* goes by, *Euphorbia marginata* appears, then is replaced by *Gutierrezia dracunculoides* in the fall. In many places *Rhus aromatica, Symphoricarpos orbiculatus, Cornus drummondii* and *Rhus glabra* are locally abundant.

ROADSIDES AND RAILROAD RIGHT-OF-WAYS

A complete list of plants found along the roadsides and railroad right-of-ways would nearly duplicate the list of plants compiled for the entire region. The vegetation of these areas consists of the border plants of whatever community the road or railroad passes.

Thickets are common along roadsides and railway right-of-ways. Common plants of these thickets are *Cornus drummondii, Prunus americana, Maclura pomifera, Rhus glabra, R. aromatica* and *Symphoricarpos orbiculatus.* Some common herbaceous plants along these areas are *Cassia fasciculata, Coronilla varia, Delphinium virescens, Euphorbia marginata, E. missurica, Kuhnia eupatorioides, Melilotus alba, M. officinalis, Oenothera speciosa* and *Saponaria officinalis.* Roadsides and railroad right-of-ways form convenient avenues of escape for many cultivated species and are likely spots for plants being introduced into a region. Cattle trucks passing along the highways afford excellent possibilities for the dispersal for seed along the route. The same is true of freight cars passing along railroad right-of-ways. Most of these introduced plants persist for just a season, but undoubtedly some have become established in the region and others will become established in the region in this manner.

CULTIVATED FIELDS

Cultivated fields are invaded by a host of plants commonly referred to as weeds. Most of these are annuals and occur in such large numbers or in such close proximity with the cultivated crop that they can't all be destroyed; therefore, a plentiful seed supply for the ensuing year is nearly always assured. The most abundant of these are *Thlaspi arvense, Chenopodium album, Kochia scoparia, Amaranthus tamariscinus, A. retroflexus, Polygonum bicorne, P. pensylvanicum, Hibiscus trionum, Digitaria sanguinalis, Setaria viridis, Panicum capillare, Abutilon theophrasti, Helianthus annuus, Ambrosia trifida, Lactuca scariola, Tribulus terrestris, Xanthium chinense, X. italicum, X. pennsylvanicum* and *X. speciosum.*

ABANDONED FIELDS

As previously mentioned, much of the Flint Hills prairie was early plowed in an attempt to practice general farming. Farming in much of the upland prairie proved to be marginal at best and many fields were abandoned and allowed to revert to native grass. These areas are easily recognized today because of the abundance of some species and the scarcity of others. *Aristida oligantha, Artemisia ludoviciana, Bromus japonicus, B. inermis, Digitaria sanguinalis, Gutierrezia dracunculoides, Panicum oligosanthes* var. *scribnerianum, Vernonia baldwinii* and *Verbascum thapsus* are common in these abandoned fields. After a long period of succession, scattered clumps of *Andropogon scoparius, Bouteloua curtipendula, Sporobolus heterolepsis* become evident and finally *Andropogon gerardi* and *Sorghastrum nutans* will reappear.

RELATIONSHIP OF THE KANSAS FLINT HILLS FLORA TO THAT OF ADJACENT AREAS

The present Kansas Flint Hills flora consists of 987 species, of which approximately 18% have been introduced. The families Aizoaceae, Caryophyllaceae, Chenopodiaceae, Cruciferae, Malvaceae, Papaveraceae, Simaroubaceae and Zygophyllaceae are represented in the area largely and in some cases totally by introduced species.

The Kansas Flint Hills area is a transition region where eastern and western species meet and, at the same time, one that has some northern and southern floristic affinities. Twenty-five per cent of the native Flint Hills species in one way or another have the limit of their distribution within the Hills. There are about 150 species of eastern North America, representing a wide-range of families, that reach the limit of their westward distribution in Kansas along the western border of the Flint Hills. Examples from this group of eastern species are *Botrychium virginianum, Erythronium albidum, Smilax herbacea, Festuca obtusa, F. paradoxa, Asimina triloba, Anemone canadensis, Podophyllum peltatum, Tilia americana, Zanthoxylum americanum, Dicentra cucullaria, Dentaria lacinata, Silene stellata, Gentiana puberulenta, Ruellia strepens, Agastache nepetoides, Stachys tenuifolia, Agrimonia pubescens, Circaea quadrisulcata, Ceanothus americanus, Rhamnus lanceolata, Aesculus glabra, Rhus copallina, Corylus americana, Ostrya virginiana, Quercus borealis, Q. marilandica, Q. muehlenbergii, Q. prinoides, Q. velutina, Eryngium yuccifolium, Osmorhiza longistylis, Polytaenia nuttallii, Campanula americana, Lobelia spicata, Helianthus hirsutus, H. laetiflorus, Aster drummondii, Solidago ulmifolia, Cacalia atriplicifolia, C. tuberosa* and *Prenanthes aspera*. There are about 50 western species that reach their eastern limit of distribution in Kansas at the eastern escarpment of the Flint Hills. The following species are examples of this group: *Heteranthera dubia, Commelina erecta, Furiena simplex, Triplasis purpurea, Chloris virgata, Ceratophyllum demersum, Callirhoe involucrata, Sphaeralcea coccinea, Croton texensis, Ditaxis mercurialina, Euphorbia missurica, Froelichia floridana, F. gracilis, Asclepias speciosa, Dalea aurea, D. enneandra, Oxytropis lambertii, Gaura coccinea, Stenosiphon linifolius, Myriophyllum pinnatum, Cur-*

curbita foetidissima, Thelesperma megapotamicum, Pyrrhopappus scaposa and *Hybanthus verticillatus.*

In addition to those species that reach their limit of distribution within the Flint Hill region, there are 100 species that are limited either in their westward or eastern distribution in Kansas by the Flint Hills but do not occur in the Hills. Fifty eastern species reach their western limits along the eastern escarpment of the Flint Hills. Examples of these species are *Adiantum pedatum, Cyperus ovularis, Scleria triglomerata, Digitaria ischaemum, Panicum clandestinum, Isopyrum biternatum, Talinum, parviflorum, Hydrophyllum virginianum, Pycnanthemum flexuosum, Tephrosia virginiana, Coreopsis palmata, Ratibida pinnata* and *Grindelia lanceolata.* Even though the western border of the Flint Hills is relatively indistinct, another 50 species seem to be limited in their eastern distribution at the western border of the area. Some of these species are *Zannichellia palustris, Carex grisea, Cyperus schweinitzii, C. filiculmis, Scirpus paludosus, Aristida longiseta, Distichlis stricta, Eragrostis oxylepis, Muhlenbergia asperifolia, Panicum obtusum, Erysium asperum, Paronychia jamesii, Talinum calycinum, Polygala alba, Asclepias pumila, Petalostemon villosum, Hymenopappus tenuifolius, Aster exilis, A. fendleri* and *Haplopappus spinulosus.*

There are about 50 species whose range, within the Flint Hills, is restricted to the southern portion, and another group of about 25 species that are restricted to the northern counties. Examples of the northern group are *Carex emoryi, Iodanthus pinnatifidus, Dentaria lacinata, Anemone virginiana, Arisaema triphyllum, Corylus americana, Hystrix patula, Cyperus diandrus, Clematis virginiana, Mimulus ringens, Impatiens biflora, Viola sororia, Quercus borealis, Juniperus virginiana* and *Parthenocissus vitacea.* The following species are examples of the group restricted to the southern area: *Camassia angusta, Nemastylis geminiflora, Luzula bulbosa, Acacia angustissma, Monarda citriodora, Cocculus carolinus, Viburnum, rufidulum, Bumelia lanuginosa, Carya illinoensis, Penstemon digitalis, Celtis tenuiflora, Ptelea trifoliata, Rhus copallina, Quercus palustris, Verbesina virginica* and *Parthenium hispidum.*

While there are no species endemic to the Kansas Flint Hills, a few have some interesting relationships. *Phlox oklahomensis* is known only from its type locality in Woodward County, Oklahoma and from Butler, Chautauqua, Cowley and Elk counties in the southern Flint Hills. Thus this phlox is largely restricted to the Flint Hills, except for the disjunct colony found on gypsiferous soils in Oklahoma.

Parthenium hispidum is relatively common in the southern Flint Hills, extends southward in Oklahoma, and is found again on dry hillsides in the Missouri Ozarks. A similar distribution is found with *Tradescantia tharpii* though it extends to the northern part of the Hills and south into Texas.

Aster sericeus is a common aster in the Flint Hills but becomes infrequent northward to North Dakota and Michigan. In northeast Kansas and northwest Missouri, it is found in dry hilltops of the Missouri River Bluffs. In the Missouri Ozarks and the Cedar Barrens of Tennessee, the species is found in bald knobs and rocky barrens. It is also known from similar areas in North Carolina and Georgia.

Stipa spartea is a northern grass common in South Dakota and eastern Nebraska, and is scattered in Iowa and northern Missouri. It is found in all the northeastern counties of Kansas, but it extends southward through the Flint Hills to Oklahoma.

In comparing the 987 species found in the Flint Hills with those found in other physiographic areas of Kansas, some interesting relationships are revealed. Work done by staff and students at the University of Kansas (unpublished) indicates the small Ozarkian section in extreme southeast Kansas has approximately 1300 species of vascular plants, of which at least 125 are known nowhere else in the state. By contrast, the flora of Morton County in extreme southwest Kansas was found by Richards (unpublished) to consist of 458 species. Morley (1964) reported 594 species for Republic County in north-central Kansas and Birkholz (1968) lists 560 species for Sumner County in south-central Kansas. Records accumulated by McGregor (unpublished) for Douglas County in northeastern Kansas indicates approximately 1100 species for that county. The flora of the Kansas Flint Hills includes approximately one half of the total number of vascular plants known to occur in Kansas.

ANNOTATED LIST

The following list includes all the native or naturalized vascular plants found in the Kansas Flint Hills. Cultivated plants have been omitted. All of the plants listed have been collected from the field, represented by voucher specimens in the University of Kansas Herbarium or included on the authority of Gates (1940).

The frequency of each species, the habitat of each and the counties in which they were found are given. For frequency, the terms abundant, common, occasional and rare have been used. A species is considered to be abundant if large numbers of individual plants can be found with ease, common if numerous individuals are found fairly often, occasional if a few scattered plants are found and, finally, rare if the species is seldom found or is known from only a single or a few records. If the plant is found in the northern counties, i.e., Marshall, Pottawatomie, Riley, Wabaunsee and Geary counties, this is designated by the statement, "found in the northern part of the area." On the other hand, if the plant is found only in the southern counties, i.e., Cowley, Butler, Chase, Lyon and Marion counties, the statement "found in the southern part of the area" is used. When the plant is distributed throughout the area the designation "found throughout the area" is used.

The families are arranged according to the traditional familiar sequence of Engler and Prantl. The nomenclature employed follows that of Gleason and Cronquist (1963) except when the species is outside their range and where more recent opinions are given in current monographs and revisions. The genera and species are arranged alphabetically within the families.

EQUISETACEAE

Equisetum arvense L. Rare, on moist streambanks and in low moist prairies. Known from the northern part.

Equisetum hyemale L. Occasional, usually found along streambanks and sometimes in moist prairies. Found in the northern part.

Equisetum laevigatum A. Br. Occasional, in low moist prairies and along drainage and seepage areas on prairie slopes. Encountered throughout the area.

OPHIOGLOSSACEAE

Botrychium virginianum (L.) Sw. Occasional, in rich wooded canyons and stream valley woods. Found throughout the area.

Ophioglossum engelmannii Prantl. Rare, in prairie areas on shallow soil above limestone outcrops and on open wooded slopes. Known from Cowley and Marion counties.

POLYPODIACEAE

Camptosorus rhizophyllus (L.) Link. Rare, grows on calcareous soil and in crevices of shaded limestone escarpments. Found in Cowley County and reported for Riley County by Gates (1940).

Cystopteris fragilis (L.) Bernh. var. *fragilis*. Rare, grows in crevices of limestone escarpments in moist wooded areas. Found in Riley and Cowley counties.

Cystopteris tennessensis Shaver. Rare, grows in the crevices of limestone escarpments in moist wooded areas. Found in Cowley and Marshall counties.

Notholaena dealbata (Pursh.) Kunze. Rare, grows in the crevices of limestone escarpments in moist wooded areas. Found in Chase, Cowley and Riley counties.

Pellaea atropurpurea (L.) Link. Occasional to locally abundant, grows in crevices of limestone rocks. Known from Cowley, Riley and Wabaunsee counties.

Pellaea glabella Mett. Rare, grows in the crevices of limestone escarpments in moist wooded areas. Known from Cowley, Geary, Riley and Wabaunsee counties.

Thelypteris palustris Schott. Rare, in marshes and floodplain woods. Reported for Pottawatomie County by Gates (1940).

Woodsia obtusa (Spreng.) Torr. Occasional, in moist canyon woods. Found in Cowley, Morris, Pottawatomie and Riley counties.

MARSILEACEAE

Marsilea mucronata A. Br. Rare, grows in roadside ditches and along the edge of ponds and marshes. Known from Butler, Chase, Cowley and Pottawatomie counties.

CUPRESSACEAE

Juniperus virginiana L. Common to abundant, in overgrazed upland prairies, on prairie slopes and in wooded canyons. Often forming dense stands in the northern part to occurring as scattered individuals in the central and southern parts of the Flint Hills.

TYPHACEAE

Typha latifolia L. Common, in wet places, along streams, impoundments, drainage areas, seepage areas and roadside ditches. Occurs throughout the area.

SPARGANIACEAE

Sparganium eurycarpum Engelm. Occasional, along the margins of streams, impoundments and other low wet places. Occurs in Riley and Wabaunsee counties.

NAJADACEAE

Potamogeton diversifolius Raf. Occasional, in impoundments. Found in Cowley County.

Potamogeton obtusifolius Mert. & Kech. Occasional, in impoundments. Reported for Riley County by Gates (1940).

Potamogeton pectinatus L. Occasional, in impoundments. Reported for Riley County by Gates (1940).

ALISMATACEAE

Alisma triviale Pursh. Rare, grows in wet roadside ditches, along streambeds and margins of impoundments. Known from Chase, Geary, Morris, Pottawatomie and Riley counties.

Echinodorus cordifolius (L.) Griseb. Rare, along muddy margins of impoundments. Found in Lyon and Riley counties.

Sagittaria ambigua J. G. Sm. Rare, growing in shallow water along the margins of ponds and lakes. Known from Cowley and Wabaunsee counties.

Sagittaria cuneata Sheldon. Rare, grows in shallow water along margins of ponds and lakes. Reported for Lyon County by Gates (1940).

Sagittaria latifolia Willd. Occasional, grows in shallow water along the margins of ponds and lakes. Found throughout the area.

Sagittaria montevidensis Cham. & Schlecht. Rare, grows in shallow water along the margins of ponds and lakes. Reported for Riley County by Gates (1940).

GRAMINEAE

Aegilops cylindrica Host. Common, along the roadsides. Found throughout the area.

Agropyron smithii Rydb. Common, in moist prairie swales and roadside ditches. Found throughout the area.

Agrostis alba L. Common, in roadside ditches and overgrazed prairies. Found in the northern part.

Agrostis hyemalis (Walt.) BSP. Occasional, in roadside ditches. Found throughout the area.

Alopecurus carolinianus Walt. Occasional, in moist prairies. Found in Cowley, Pottawatomie and Riley counties.

Alopecurus myosuroides Huds. Rare, in waste places and railway banks. Reported for Riley County by Gates (1940).

Alopecurus pratensis L. Rare, in meadows and waste places. Reported for Riley County by Gates (1940).

Andropogon gerardi Vitman. Abundant, in well-managed upland prairies, on north-facing prairie slopes, in prairie canyons and open lowland woods. Found throughout the area.

Andropogon ischaemum L. Occasional, introduced along prairie roadsides and in overgrazed prairies. Known from Wabaunsee County.

Andropogon saccharoides Swartz. Occasional to common, along roadsides and sometimes in overgrazed prairies. Common in the southern part becoming occasional in the northern part of the region.

Andropogon scoparius Michx. Abundant in well-drained upland prairie and on well-drained and south-facing prairie slopes. Known throughout the area.

Andropogon virginicus L. Occasional, in overgrazed prairies. Reported for Lyon and Riley counties by Gates (1940).

Aristida basiramea Engelm. Rare, in dry overgrazed prairies. Reported for Pottawatomie and Riley counties by Gates (1940).

Aristida longiseta Steud. Rare, in dry overgrazed prairies. Reported for Riley County by Gates (1940).

Aristida oligantha Michx. Common, on clay-pan areas and in overgrazed prairies. Found throughout the area.

Aristida purpurascens Poir. Rare, in dry overgrazed prairie. Reported for Riley County by Gates (1940).

Avena sativa L. Occasional, escaped or introduced along roadsides and in cultivated fields. Known from Cowley County.

Bouteloua curtipendula Michx. Abundant, in upland prairies and on prairie slopes. Found throughout the Flint Hills.

Bouteloua gracilis (HBK.) Lag. Occasional, in overgrazed prairies and along roadsides. Known throughout the area.

Bouteloua hirsuta Lag. Occasional to common, in overgrazed prairies. Known throughout the area.

Bromus catharticus Vahl. Rare, in overgrazed prairies and waste places. Reported for Riley County by Gates (1940).

Bromus inermis Leyss. Common, introduced in roadside ditches, overgrazed prairies and cultivated for hay. Known throughout the area.

Bromus japonicus Thunb. Common, along roadsides and in overgrazed prairies. Known throughout the area.

Bromus mollis L. Rare, along roadsides and in waste places. Reported for Riley County by Gates (1940).

Bromus purgans L. Occasional, in moist rocky woods. Found in the northern part.

Bromus secalinus L. Occasional, in overgrazed prairies and waste places. Known throughout the area.

Bromus tectorum L. Common, in roadside ditches, in cultivated and abandoned fields. Found throughout the region.

Buchloe datyloides (Nutt.) Engelm. Common to locally abundant, in overgrazed upland prairies. Found throughout the area.

Calamovilfa gigantea (Nutt.) Lamson-Scribner. Rare, on sand dunes along the Kansas River. Reported for Riley County by Gates (1940).

Calamovilfa longifolia (Hook.) Scribner. Rare, on sandy areas along streambanks. Reported for Geary, Pottawatomie and Riley counties by Gates (1940).

Cenchrus longispinus (Hack.) Fern. Common, in roadside ditches, waste places and severely overgrazed prairies. Found throughout the area.

Chloris verticillata Nutt. Common, in roadside ditches, waste places and overgrazed prairies. Occurs throughout the area.

Chloris virgata Sw. Occasional, along roadsides and in overgrazed prairies. Found in the southern part.

Cinna arundinacea L. Occasional, in moist lowland woods. Reported for Pottawatomie and Riley counties by Gates (1940).

Cynodon dactylon (L.) Pers. Occasional, cultivated in lawns and occasionally escaped to roadsides and overgrazed prairies. Found throughout the area.

Dactylis glomerata L. Occasional, in cultivated fields, meadows, and waste places. Found in the northern part.

Danthonia spicata (L.) Beauv. Rare, grows in rocky soil along limestone escarpments. Known from Marshall County.

Diarrhena americana Beauv. Occasional, in rich stream valley woods. Found throughout the area.

Digitaria filiformis (L.) Koel. Rare, on sandy soil along streambeds. Reported for Pottawatomie County by Gates (1940).

Digitaria ischaemum (Schreb.) Muhl. Occasional, in cultivated fields and waste places. Reported for Pottawatomie and Riley counties by Gates (1940).

Digitaria sanguinalis (L.) Scop. Abundant, along roadsides, in cultivated fields and on sandy streambanks. Found throughout the area.

Distichlis stricta (Torr.) Rydb. Rare, in waste places with alkaline soils. Known throughout the area.

Echinochloa crusgalli (L.) Beauv. Abundant, along roadsides, streambanks, ponds, reservoirs and in cultivated fields. Found throughout the area.

Eleusine indica (L.) Gaertn. Common, along roadsides, in cultivated ground and other waste places. Encountered throughout the area.

Elymus canadensis L. Common, in roadside ditches, overgrazed prairies, prairie canyons and along streambanks. Known throughout the area.

Elymus villosus Muhl. Occasional, in floodplain woods and on streambanks. Found in the northern part.

Elymus virginicus L. Common, in moist lowland prairies, canyon woods along streambanks. Encountered throughout the area.

Eragrostis capillaris (L.) Nees. Occasional, in dry overgrazed prairies, open woods and waste places. Reported for Morris, Riley and Wabaunsee counties by Gates (1940).

Eragrostis cilianensis (All.) Link. Abundant, along roadsides, in cultivated fields and other waste places. Known throughout the area.

Eragrostis hypnoides (Lam.) BSP. Occasional, dense mats are found growing along moist streambanks and margins of impoundments. Known from Riley and Pottawatomie counties.

Eragrostis oxylepis (Torr.) Torr. Rare, occurs in dry sandy prairies. Reported for Riley and Pottawatomie counties by Gates (1940).

Eragrostis pectinacea (Michx.) Nees. Occasional, along impoundments, streambanks, in cultivated fields and waste places. Found throughout the area.

Eragrostis pilosa (L.) Beauv. Rare, in cultivated fields and waste places. Reported for Chase County by Gates (1940).

Eragrostis poaeoides Beauv. Rare, cultivated fields and waste places. Reported for Geary County by Gates (1940).

Eragrostis spectabilis (Pursh.) Steud. Common, along roadsides and in overgrazed prairies. Known throughout the region.

Eragrostis trichodes (Nutt.) Wood. Occasional, in sandy soil along rivers and streambeds. Reported for Geary, Riley and Pottawatomie counties by Gates (1940).

Eriochloa contracta Hitchc. Common, in roadside ditches, cultivated fields and low wet places. Encountered throughout the area.

Festuca elatior L. Occasional, in prairie hay meadows, open lowland woods and in roadside ditches. Reported for Marshall and Riley counties by Gates (1940).

Festuca obtusa Biehler. Occasional, in floodplain woods. Found in the northern part.

Festuca octoflora Walt. Common, in overgrazed upland prairies and on prairie slopes. Found throughout the area.

Festuca paradoxa Desv. Common, in roadside ditches, low moist prairies and open lowland woods. Known from the northern part.

Glyceria striata (Lam.) Hitchc. Occasional, in low wet areas along impoundments and wet lowland prairies. Found in the northern part.

Hordeum jubatum L. Common, along roadsides and in overgrazed upland prairies. Known in the northern part.

Hordeum pusillum Nutt. Common, in overgrazed upland prairies and on prairie slopes. Encountered throughout the region.

Koeleria cristata (L.) Pers. Common, in well-managed upland prairies. Found throughout the area.

Leersia oryzoides (L.) Sw. Rare, in wet places along streams and impoundments. Reported for Pottawatomie and Riley counties by Gates (1940).

Leersia virginica Willd. Common, in wet places along streams and impoundments. Found throughout the region.

Leptochloa fascicularis (Lam.) Gray. Occasional, along streambeds, drainage areas and margins of impoundments. Known from the northern and southern part of the area.

Leptoloma cognatum (Schultes) Chase. Common, in rocky roadside ditches and overgrazed prairies. Found throughout the area.

Lolium perenne L. Rare, introduced into cultivated areas and waste places. Reported for Marion and Riley counties by Gates (1940).

Lolium temulentum L. Rare, introduced into cultivated areas and waste places. Reported for Riley County by Gates (1940).

Melica nitens Nutt. Rare, in rocky soil of wooded canyons. Known from Riley and Geary counties.

Muhlenbergia brachyphylla Bush. Common, in floodplain woods and along streambanks. Found throughout the area.

Muhlenbergia cuspidata (Torr.) Rydb. Common, on prairie slopes and in overgrazed upland prairies. Known from throughout the area.

Muhlenbergia frondosa (Poir.) Fern. Rare, in low ground along roadsides, fence rows and other waste places. Collected once in Marshall County.

Muhlenbergia mexicana (L.) Trin. Common, in floodplain woods and along streambanks. Found in the northern part.

Muhlenbergia racemosa (Michx.) BSP. Common, in moist prairie canyons and open floodplain woods. Known from the northern part.

Muhlenbergia schreberi Gmel. Common, in floodplain woods. Known from Chase, Pottawatomie and Riley counties.

Muhlenbergia sobolifera (Muhl.) Trin. Rare, in wooded canyons on rocky soil. Reported from Geary and Riley counties by Gates (1940).

Muhlenbergia sylvatica Torr. Occasional, in floodplain woods and along streambanks. Known from Geary, Pottawatomie and Riley counties.

Panicum capillare L. Abundant, along roadsides, in cultivated fields, waste places and severely overgrazed prairies. Found throughout the area.

Panicum clandestinum L. Rare, low moist wooded areas. Reported for Pottawatomie County by Gates (1940).

Panicum dichotomiflorum Michx. Common, along roadsides, in cultivated fields and in overgrazed prairies. Found throughout the area.

Panicum lanuginosum Ell. var. *fasciculatum* (Torr.) Fern. Occasional, in well-managed upland prairies and in open wooded areas. Known from Cowley, Pottawatomie and Riley counties.

Panicum oligosanthes Schult. var. *scribnerianum* (Nash.) Fern. Common, in overgrazed upland prairies, on prairie slopes and in open wooded canyons. Found throughout the area.

Panicum perlongum Nash. Common, in well-managed upland prairies. Known from Geary, Morris and Riley counties.

Panicum praecocius Hitchc. & Chase. Rare, in overgrazed upland prairies. Reported from Geary, Pottawatomie and Riley counties by Gates (1940).

Panicum sphaerocarpon Ell. Occasional, in well-managed upland prairies. Known from Marshall and Cowley counties.

Panicum virgatum L. Abundant, in upland prairies, prairie canyons and often used in seed mixtures to reseed abandoned fields and overgrazed prairies. Known throughout the area.

Panicum wilcoxianum Vasey. Rare, in well-managed upland prairies. Reported for Pottawatomie and Riley counties by Gates (1940).

Paspalum ciliatifolium Michx. Common, along roadsides and in overgrazed upland prairies. Known from throughout the region.

Paspalum pubiflorum Rupr. Common, along roadsides and in overgrazed prairies. Found in the southern part.

Phalaris arundinacea L. Rare, along streambanks and in low wet places. Reported for Pottawatomie County by Gates (1940).

Phalaris canariensis L. Rare, introduced overgrazed prairies and in waste places. Known from Butler, Lyon and Morris counties.

Phleum pratense L. Common, introduced along roadsides, in prairie hay meadows, overgrazed prairies and waste places. Found throughout the area.

Phragmites communis Trin. Rare, grows in large colonies in swamps, marshes and at the edge of impoundments. Reported from Pottawatomie County by Gates (1940).

Poa annua L. Rare, in lawns, waste places and cultivated ground. Reported for Pottawatomie County by Gates (1940).

Poa pratensis L. Common, in overgrazed upland prairies, prairie hay meadows, on prairie slopes and in open wooded canyons. Known throughout the area.

Poa sylvestris Gray. Occasional, in floodplain woods and sometimes in the drier wooded canyons. Known from Riley and Pottawatomie counties.

Polypogon monspeliensis (L.) Desf. Occasional, grows in sandy soil along Arkansas River in Cowley County. Known from Cowley County.

Schedonnardus paniculatus (Nutt.) Trel. Common, in roadside ditches, cultivated fields and severely overgrazed prairies. Found throughout the area.

Setaria geniculata (Lam.) Beauv. Common, along roadsides, in cultivated fields, waste places and severely overgrazed prairies. Known throughout the area.

Setaria faberii Herrm. Common, in roadside ditches, cultivated fields, waste places and in open floodplain woods. Found throughout the region.

Setaria italica (L.) Beauv. Rare, sometimes cultivated and escaping along roadsides. Reported for Cowley, Pottawatomie, Riley and Wabaunsee counties by Gates (1940).

Setaria lutescens (Weigel) Hubb. Common, along roadsides, in cultivated fields, waste places and overgrazed prairies. Found throughout the area.

Setaria verticillata (L.) Beauv. Rare, in waste places and around dwellings. Reported for Riley County by Gates (1940).

Setaria viridis (L.) Beauv. Common, along roadsides, in cultivated fields, waste places, overgrazed prairies and open wooded canyons. Found throughout the area.

Sorghastrum nutans (L.) Nash. Abundant, in well-managed upland prairies, on moist north-facing prairie slopes, in prairie canyons and in open wooded canyons. Found throughout the area.

Sorghum halepense (L.) Pers. Common, in roadside ditches, in cultivated fields and other waste places. Occurs throughout the region.

Spartina pectinata Link. Common, in wet roadside ditches, along drainage areas and along the margins of impoundments. Encountered throughout the area.

Sphenopholis obtusata (Michx.) Scribn. Occasional, in well-managed upland prairies, prairie hay meadows and sometimes in overgrazed prairies. Encountered more often in the northern part becoming very rare in the southern part.

Sporobolus asper (Michx.) Kunth. Common, on prairie slopes and in open wooded canyons. Occurs throughout the area.

Sporobolus clandestinus (Biehler) Hitchc. Rare, in sandy fields, prairies. Reported for Pottawatomie and Riley counties by Gates (1940).

Sporobolus cryptandrus (Torr.) Gray. Common, on roadside banks, in overgrazed upland prairies and on prairie slopes. Found throughout the area.

Sporobolus heterolepis Gray. Common, in well-managed upland prairies, prairie canyons and wooded canyons. Found throughout the area but much more common in the northern part.

Sporobolus neglectus Nash. Occasional, on roadside banks and on prairie slopes. Encountered throughout the area.

Sporobolus vaginiflorus (Torr.) Wood. Rare, on roadside banks and on shallow soil along limestone escarpments. Known from Butler, Morris, Pottawatomie and Riley counties.

Stipa spartea Trin. Occasional, grows in small patches in well-managed upland prairies and in prairie hay meadows. Occurs in the northern and southern counties of the Flint Hills but not in the central counties.

Triodia flava (L.) Smyth. Common, along roadsides, in waste places, overgrazed prairies and open wooded areas. Found throughout the area.

Triplasis purpurea (Walt.) Chapm. Rare, occurs in sandy places. Reported for Riley County by Gates (1940).

Tripsacum dactyloides L. Common, well-managed upland prairies, prairie hay meadows, prairie canyons and open lowland woods. Found throughout the area.

Trisetum flavescens (L.) Beauv. Rare, occurs in waste places. Reported for Riley County by Gates (1940).

Uniola latifolia Michx. Occasional, in floodplain woods. Known Cowley, Geary, Pottawatomie, Riley and Wabaunsee counties.

CYPERACEAE

Bulbostylis capillaris (L.) C. B. Clarke. Rare, in moist prairie swales and in sandy soils along streams. Reported for Pottawatomie County by Gates (1940).

Carex aggregata Mackenzie. Occasional, on open wooded hillsides and in open wooded canyons. Found only in the northern part.

Carex amphibola Steud. Common, in rich woods and on wooded north-facing slopes. Occurs throughout the area.

Carex annectans Bickn. var. *annectans*. Common, in wet areas of upland prairies and in prairie canyons. Known from Lyon County.

Carex annectans Bickn. var. *xanthocarpa* (Bickn.) Wieg. Occasional, in wet areas of upland prairies and in prairie canyons. Known from Lyon County.

Carex artitecta Mackenzie. Rare, on wooded canyon slopes. Reported from Pottawatomie and Riley counties by Gates (1940).

Carex bicknellii Britt. Occasional, in upland prairie and in prairie canyons. Known from Lyon, Riley and Wabaunsee counties.

Carex blanda Dewey. Common, in wooded areas. Occurs throughout the area.

Carex brevior (Dewey) Mackenzie. Common, in upland prairies, on prairie slopes and in prairie canyons. Found throughout the area.

Carex bushii Mackenzie. Common, in upland prairies, in prairie canyons, and sometimes found on open wooded slopes. Known from Butler, Chase, Lyon and Wabaunsee counties.

Carex cephalophora Muhl. var. *cephalophora*. Rare, on open wooded slopes, and sometimes found in open lowland woods. Known from Marshall and Riley counties.

Carex crawei Dewey. Occasional, in wet places in upland prairies and along the margins of impoundments. Found in Cowley County.

Carex crus-corvi Shuttlew. Rare, in low wet places and in floodplain woods. Known from Lyon and Wabaunsee counties.

Carex davisii Schwein. & Torr. Rare, in floodplain woods. Reported for Riley County by Gates (1940).

Carex eleocharis Bailey. Rare, in upland prairie. Reported for Riley County by Gates (1940).

Carex emoryi Dewey. Occasional, on streambanks and in floodplain woods. Found in the northern part.

Carex frankii Kunth. Rare, along wet places in upland prairies, on streambanks and along margins of impoundments. Known from Chase, Lyon and Morris counties.

Carex gravida Bailey. Common, in upland prairies, on prairie slopes, in prairie canyons and less commonly in open wooded areas. Found throughout the area.

Carex heliophila Mackenzie. Occasional, on dry wooded slopes. Reported for Pottawatomie, Riley and Wabaunsee counties by Gates (1940).

Carex hyalinolepsis Steud. Rare, in wet places along streams, impoundments and roadside ditches. Found in Cowley and Pottawatomie counties.

Carex hystricina Muhl. Common, in wet areas along streams, impoundments and seepage areas. Found in the northern part.

Carex interior Bailey. Rare, in swampy prairie areas and along seepage areas along limestone escarpments. Reported from Riley County by Gates (1940).

Carex laeviconica Dewey. Rare, in wet soil of floodplain woods, along streams and in low wet prairies. Known from Pottawatomie and Riley counties.

Carex lanuginosa Michx. Common, in wet swales in upland prairies, along seepage areas and in moist prairie canyons. Found in the northern part.

Carex meadii Dewey. Common, in upland prairies, prairie hay meadows and prairie canyons. Found throughout the area.

Carex molesta Mackenzie. Occasional, in wet places, in moist upland prairies, on moist open wooded slopes and in prairie canyons. Found in Chase, Cowley and Marshall counties.

Carex muhlenbergia Schkuhr. var. *australis* Olney. Common, in upland prairies, and on open wooded slopes. Encountered throughout the area.

Carex normalis Mackenzie. Common, in wet places, along drainage areas, in moist floodplain woods and along streambanks. Found throughout the area.

Carex oligocarpa Schkuhr. Rare, in floodplain woods and along streambanks. Found in Wabaunsee County.

Carex praegracilis W. Boot. Rare, in upland prairies. Reported for Wabaunsee County by Gates (1940).

Carex stipata Muhl. Rare, along streambanks, in floodplain woods and in wet lowland prairies. Reported for Riley County by Gates (1940).

Carex vulpinoidea Michx. Common, in wet places, in upland prairies, along margins of impoundments, along streambanks and in floodplain woods. Found throughout the area.

Cyperus acuminatus Torr. & Hook. Common, along wet places, along streambanks, margins of impoundments, and in wet cultivated ground. Found throughout the area.

Cyperus aristatus Rottb. Common, along wet places in prairies, margins of impoundments, streams and in low wet cultivated ground. Occurs throughout the area.

Cyperus diandrus Torr. Rare, in wet places along limestone escarpments, along margins of impoundments and streambeds. Known from Pottawatomie and Riley counties.

Cyperus erythrorhizos Muhl. Occasional, in wet places, along margins of impoundments and streambeds. Found in Butler, Lyon and Riley counties.

Cyperus esculentus L. Common, in wet places, in prairie swales, along margins of impoundments, streams and in low moist cultivated ground. Found in the northern part.

Cyperus ferruginescens Boeckl. Common, in wet places, in prairie swales, along margins of impoundments and streambeds. Found throughout the area.

Cyperus filiculmis Vahl. Common, in upland prairies, on gentle-sloping prairie hillsides, in open woods on prairie slopes. Occurs throughout the area.

Cyperus ovularis (Michx.) Torr. Rare, in prairies, in dry open wooded slopes and along streams. Found in Cowley County.

Cyperus schweinitzii Torr. Rare, sandy low ground along streams and ponds. Reported for Riley County by Gates (1940).

Cyperus setigerus Torr. & Hook. Common, in wet places, along the margins of impoundments and streams. Found in the southern part.

Cyperus strigosus L. Common, in wet places, along the margins of impoundments and streams. Found in the northern part.

Eleocharis calva Torr. Common, along margins of impoundments, streams, sloughs and in wet prairies. Found in Marshall, Pottawatomie and Wabaunsee counties.

Eleocharis compressa Sulliv. Common, in wet places, in prairie drainage areas, roadside ditches and along margins of impoundments. Occurs throughout the area.

Eleocharis macrostachya Britt. Common, along margins of impoundments, streams, sloughs and in wet prairies. Found in the northern part.

Eleocharis montevidensis Kunth. Rare, in wet sandy places along streams and impoundments. Known from Cowley County.

Eleocharis obtusa (Willd.) Schultes. Occasional, in muddy areas along streams and impoundments. Reported for Morris and Pottawatomie counties by Gates (1940).

Fimbristylis puberula (Michx.) Vahl. Common, in upland prairies, prairie hay meadows, prairie canyons and sometimes in open wooded areas. Collected from Butler, Cowley, Pottawatomie and Riley counties.

Fuirena simplex Vahl. Rare, grows in wet soil along springs, seepage areas and streams. Found in Cowley, Pottawatomie and Riley counties.

Hemicarpha micrantha (Vahl.) Pax. Rare, grows in sandy soil. Reported for Pottawatomie County by Gates (1940).

Scirpus americanus Pers. Rare, grows in sandy soil along the Kansas River. Reported for Riley County by Gates (1940).

Scirpus atrovirens Willd. Common, grows in wet roadside ditches, along margins of impoundments and open streambanks. Found throughout the area.

Scirpus lineatus Michx. Common, in wet soil of prairie drainage areas, roadside ditches, margins of impoundments and along streambanks. Encountered throughout the area.

Scirpus validus Vahl. Common, in wet soil of roadside ditches and along the margins of impoundments. Found throughout the area.

ARACEAE

Acorus calamus L. Rare, sometimes introduced in swampy areas along margins of ponds and streams. Reported for Pottawatomie and Riley counties by Gates (1940)

Arisaema dracontium (L.) Schott. Rare, in moist stream valley woods. Encountered throughout the area.

Arisaema triphyllum (L.) Schott. Rare, in moist stream valley woods. Reported for Pottawatomie County by Gates (1940).

LEMNACEAE

Lemna minor L. Occasional, in impoundments and slow-moving streams. Reported for Geary County by Gates (1940).

Lemna perpusilla Torr. Occasional, in impoundments and slow-moving streams. Reported for Riley County by Gates (1940).

Spirodela polyrhiza (L.) Schleid. Occasional, in impoundments and slow-moving streams. Known from Cowley, Pottawatomie and Riley counties.

Wolffia columbiana Karst. Occasional, in impoundments. Reported for Geary County by Gates (1940).

COMMELINACEAE

Commelina erecta L. Rare, in stream valley woods and along streambanks. Found in Pottawatomie and Riley counties.

Commelina virginica L. Common, in wooded canyons, floodplain woods and in thickets along the roadsides. Found throughout the area.

Tradescantia bracteata Small. Common, in overgrazed upland prairies, prairie hay meadows, along roadsides and railway right-of-ways. Occurs throughout the area.

Tradescantia ohiensis Raf. Common, in overgrazed upland prairies, prairie hay meadows, along the roadsides, railway right-of-ways and sometimes in open wooded areas. Encountered throughout the area.

Tradescantia tharpii Anderson & Woodson. Common, in overgrazed upland prairies, on gentle prairie slopes and in prairie canyons. Found throughout the Flint Hills.

PONTEDERIACEAE

Heteranthera dubia (Jacq.) MacM. Occasional, grows at the edge of streams or impoundments, either in shallow water or on the mud. Reported for Riley County by Gates (1940).

Heteranthera limosa (Sw.) Willd. Occasional, grows at the edge of streams or impoundments, either in shallow water or on the mud. Reported for Morris and Riley counties by Gates (1940).

Heteranthera reniformis R. & P. Occasional, grows at the edge of streams or impoundments, either in shallow water or on the mud. Reported for Pottawatomie and Riley counties by Gates (1940).

JUNCACEAE

Juncus diffusissimus Buckl. Rare, grows in wet soil in roadside ditches, seepage areas, along margins of impoundments and streams. Known from Pottawatomie County.

Juncus dudleyi Wieg. Common, in wet prairies, along seepage areas, drainage areas, margins of impoundments and streams. Encountered throughout the area.

Juncus interior Wieg. Common, in moist prairies, along seepage areas, drainage areas, margins of impoundments and streams. Occurs throughout the area.

Juncus marginatus Lam. Rare, in moist prairies and prairie hay meadows. Found in Cowley and Pottawatomie counties.

Juncus torreyi Coville. Common, in wet prairies, along seepage areas, drainage areas, margins of impoundments and streams. Known from throughout the area.

Luzula bulbosa (Wood) Rydb. Rare, in open wooded areas, on rocky prairie slopes and in overgrazed upland prairies. Known from Cowley County.

LILIACEAE

Allium canadense L. var. *canadense.* Occasional, in open floodplain woods, prairie canyons, prairie hay meadows, upland prairies, along roadsides and railway right-of-ways. Found in Butler and Cowley counties.

Allium canadense L. var. *fraseri.* Owenby. Common, in open floodplain woods, prairie canyons, prairie hay meadows, upland prairies, along roadsides and railway right-of-ways. Found throughout the area.

Allium canadense L. var. *lavendulare* (Bates) Owenby & Ashe. Occasional, in open floodplain woods, prairie canyons, prairie hay meadows, upland prairies, along roadsides and railroad right-of-ways. Found in the southern part.

Allium stellatum Ker. Common, in rocky upland prairies, and on rocky prairie slopes. Found in the northern part of the area.

Androstephium coerulem (Scheele) Greene. Occasional, in rocky upland prairies and on rocky, prairie slopes. Found in Butler, Cowley, Geary and Marion counties.

Asparagus officinalis L. Common, escapes from cultivation into roadside ditches, cultivated fields and other such waste places. Occurs throughout the area.

Camassia angusta (Engelm. & Gray) Blankinship. Occasional, in rocky upland prairies and on rocky prairie slopes. Occurs in Butler and Cowley counties.

Camassia scilloides (Raf.) Cory. Occasional, in open wooded areas, prairie canyons, prairie hay meadows and well-managed upland prairies. Known from Cowley County.

Erythronium albidum Nutt. Common, in floodplain woods and wooded canyons. Found in the northern part of the area and in Cowley County.

Erythronium mesochoreum Knerr. Common, in rocky upland prairies, on rocky prairie slopes and in open woods on prairie slopes. Found in Butler, Geary, Lyon, Morris and Wabaunsee counties.

Nothoscordum bivale (L.) Britt. Common, in upland prairies, on prairie slopes and in open wooded areas on prairie slopes. Found throughout the area.

Polygonatum biflorum (Walt.) Ell. Common, in floodplain woods and on wooded slopes. Found throughout the area.

Smilacina racemosa (L.) Desf. Rare, in rocky wooded areas. Reported for Riley County by Gates (1940).

Smilacina stellata (L.) Desf. Rare, in moist floodplain woods. Reported for Riley and Pottawatomie counties by Gates (1940).

Smilax herbacea L. var. *lasioneuron* (Small) Rydb. Common, in stream valley woods and wooded canyons. Found throughout the area.

Smilax hispida Muhl. Common, in floodplain woods and wooded canyons. Occurs throughout the area.

Yucca glauca Nutt. Occasional, in rocky upland prairies, on rocky prairie slopes and on road-cuts. Occurs throughout the area.

Zygadenus nuttallii Gray. Occasional, in moist upland prairies, on prairie slopes and in prairie canyons. Encountered throughout the area.

IRIDACEAE

Belamcanda chinensis (L.) DC. Rare, escaped from cultivation and established in prairies and along roadsides. Reported for Cowley, Riley and Wabaunsee counties by Gates (1940).

Nemastylis geminiflora Nutt. Rare, in well-managed upland prairies, prairie hay meadows and open-wooded areas. Known from Cowley County.

Sisyrinchium campestre Bickn. var. *campestre*. Common, in upland prairies, prairie hay meadows, on prairie slopes, in prairie canyons and in open wooded areas. Found throughout the area.

Sisyrinchium campestre Bickn. var. *kansanum* Bickn. Occasional, in upland prairies, prairie hay meadows, on prairie slopes, in prairie canyons and in open wooded areas. Occurs throughout the area.

ORCHIDACEAE

Habenaria leucophaea (Nutt.) Gray. Rare, in wet prairie areas. Reported for Lyon and Riley counties by Gates (1940).

Liparis loeselii (L.) Richard. Rare, in woods and thickets. Reported for Pottawatomie County by Gates (1940).

Spiranthes cernua (L.) Rich. Rare, in moist upland prairies, prairie hay meadows, and prairie canyons. Found in Lyon and Riley counties.

Spiranthes vernalis Engelm. & Gray. Rare, in moist upland prairies and wet prairie hay meadows. Found in Lyon County and reported for Cowley, Morris and Riley counties by Gates (1940).

SALICACEAE

Populus alba L. Occasional, escapes from cultivation to along streams, fence rows and roadsides. Collected from Riley and Wabaunsee counties.

Populus deltoides Marsh. (including *P. sargentii* Dode). Common, in floodplain woods. Occurs throughout the area.

Salix amygdaloides Anderss. Common, in floodplain woods and along streambanks. Found in Geary, Marshall, Morris, Pottawatomie, Riley and Wabaunsee counties.

Salix caroliniana Michx. Common, in floodplain woods and along streambanks. Found in Butler, Chase, Cowley, Geary, and Wabaunsee counties.

Salix eriocephala Michx. Rare, in alluvial soil along streams. Reported for Geary, Morris, Pottawatomie and Riley counties by Gates (1940).

Salix humilis Marsh. var. *microphylla* (Anderss.) Fern. Occasional, in upland prairies, on rocky prairie slopes, in open areas in wooded canyons and along prairie roadsides. Known from Marshall, Pottawatomie and Riley counties.

Salix interior Rowlee. Common, in floodplain woods and along streambanks. Found throughout the area.

Salix nigra L. Common, in floodplain woods and along streambanks. Occurs throughout the area.

Salix rigida Muhl. Occasional, in alluvial soil along streams. Known from Marshall, Morris and Riley counties.

JUGLANDACEAE

Carya cordiformis (Wang.) K. Koch. Common, in rich woods along streams, drainage areas and in moist wooded canyons. Found throughout the area.

Carya illinoensis (Wang.) K. Koch. Rare, in floodplain woods and often cultivated in low places. Known from Cowley County.

Carya laciniosa (Michx.) Loud. Occasional, in rich woods along streams. Found in Cowley County.

Carya ovata (Mill.) K. Koch. Rare, in rich woods along streams. Reported for Riley County by Gates (1940).

Juglans nigra L. Common, in rich wooded canyons, rich woods along streams and sometimes occurring as scattered individuals in upland areas. Found throughout the area.

CORYLACEAE

Corylus americana Walt. Occasional, in wooded canyons and sometimes in floodplain woods. Known from Pottawatomie, Riley and Wabaunsee counties.

Ostrya virginiana (Mill.) K. Koch. Occasional, in wooded canyons and along margins of floodplain woods. Found in Pottawatomie, Riley and Wabaunsee counties.

FAGACEAE

Quercus borealis Michx. Occasional, on well-drained rocky wooded slopes. Known from Geary, Pottawatomie and Riley counties.

Quercus macrocarpa Michx. Common, on rocky wooded slopes and in wooded canyons. Occurs throughout the area.

Quercus marilandica Muenchh. Rare, on rocky wooded slopes. Known from Pottawatomie and Riley counties.

Quercus muehlenbergii Engelm. Common, on rocky wooded slopes. Found throughout the area.

Quercus palustris Muenchh. Rare, in floodplain woods along the Arkansas River. Known only from Cowley County.

Quercus prinoides Willd. Common, on rocky wooded slopes and in wooded canyons. Found throughout the area.

Quercus shumardii Buckl. Rare, on rocky wooded slopes. Known only from Cowley County.

Quercus stellata Wang. Rare, in sandy soil of upland wooded areas. Reported for Riley County by Gates (1940).

Quercus velutina Lam. Occasional, on rocky wooded slopes and in well-drained soil along streams. Known from Cowley, Pottawatomie and Riley counties.

ULMACEAE

Celtis laevigata Willd. var. *texana* Sarg. Rare, in rocky wooded canyons. Known from Cowley County.

Celtis occidentalis L. var. *canina* (Raf.) Sarg. Rare, in rocky wooded canyons. Known from Lyon County.

Celtis occidentalis L. var. *occidentalis*. Common in rocky wooded canyons and wooded stream valleys. Occurs throughout the area.

Celtis occidentalis L. var. *pumila* (Pursh.) Gray. Occasional, in rocky wooded canyons and wooded stream valleys. Found throughout the area.

Celtis tenuifolia Nutt. var. *georgiana* (Small) Fern. & Schub. Rare, in rocky wooded canyons. Known from Cowley County.

Ulmus americana L. Common, in rocky wooded canyons and in floodplain woods. Found throughout the area.

Ulmus pumila L. Occasional, escapes from cultivation to along roadsides, in wooded canyons and floodplain woods. Occurs throughout the area.

Ulmus rubra Muhl. Common, in rocky wooded canyons and in floodplain woods. Found throughout the area.

MORACEAE

Cannabis sativa L. Common to abundant, in waste places, along moist railroad right-of-ways and in open floodplain woods. Found in the northern part of the area.

Humulus lupulus L. Occasional, in waste ground, in open wooded areas, and along railroad right-of-ways. Occurs throughout the area.

Maclura pomifera (Raf.) Scheid. Common, in floodplain woods, margins of woods, as scattered individuals in grazed prairies, along fence rows and roadsides. Occurs throughout the area.

Morus alba L. Common, in moist woods along streams, along fence rows and grazed prairies. Known from Lyon, Marshall, Morris, Riley and Wabaunsee counties.

Morus rubra L. Common, in floodplain woods, wooded canyons, along fence rows and grazed prairies. Found throughout the area.

URTICACEAE

Boehmeria cylindrica (L.) Sw. Rare, in floodplain woods and low wet ground. Reported for Marshall and Pottawatomie counties by Gates (1940).

Laportea canadensis (L.) Wedd. Occasional, in moist stream valley woods. Found throughout the area.

Parietaria pennsylvanica Muhl. Occasional to common, in wooded canyons and stream valley woods. Occurs throughout the area.

Pilea pumila (L.) Gray. Occasional, in moist stream valley woods. Found throughout the area.

Urtica dioica L. var. *procera* (Muhl.) Wedd. Common, in moist stream valley woods. Occurs throughout the area.

SANTALACEAE

Comandra umbellata (L.) Nutt. subsp. *pallida* (A. DC) Piehl. Rare, in rocky prairie areas and in rocky wooded canyons. Collected once by W. H. Horr in Cowley County.

Comandra umbellata (L.) Nutt. subsp. *umbellata*. Rare, in rocky wooded canyons. Reported for Pottawatomie and Wabaunsee counties by Gates (1940).

POLYGONACEAE

Eriogonum annuum Nutt. Rare, in prairies on sandy soils. Known from Riley and Cowley counties.

Polygonum aviculare L. Common, in waste places, lawns, along roadsides, about farmyards and in severely overgrazed prairies. Found throughout the area.

Polygonum bicorne Raf. Occasional, in wet low ground along drainage areas and streams. Found throughout the area.

Polygonum coccineum Muhl. Occasional, in water at the edge of impoundments, streams and roadside ditches. Occurs throughout the area.

Polygonum convolvulus L. Occasional, along roadsides, railway right-of-ways, in cultivated fields and waste ground. Occurs throughout the area.

Polygonum erectum L. Occasional, in overgrazed prairies, waste ground along roadsides and railway right-of-ways. Encountered throughout the area.

Polygonum hydropiper L. Rare, in cultivated fields, along prairie drainage areas, margins of impoundments and streams. Reported for Riley County by Gates (1940).

Polygonum hydropiperoides Michx. Rare, in wet ground along impoundments, seepage areas and streams. Reported for Riley County by Gates (1940).

Polygonum lapathifolium L. Common, in low wet alluvial soil along drainage areas, impoundments and streams. Occurs throughout the area.

Polygonum pennsylvanicum L. Common, in wet alluvial soil along drainage areas, impoundments and streams. Found throughout the area.

Polygonum persicaria L. Common, in waste ground, cultivated fields, moist overgrazed prairies and along streams. Encountered throughout the area.

Polygonum punctatum Ell. Common, in alluvial soil along drainage areas, impoundments and streams. Occurs throughout the area.

Polygonum ramosissimum Michx. Occasional, in upland and canyon prairies. Known throughout the area.

Polygonum scandens L. Common, in floodplain woods and wooded canyons. Found throughout the area.

Polygonum tenue Michx. Occasional, in rocky upland prairie and on rocky prairie slopes. Known from Chase, Marion, Morris, Pottawatomie and Wabaunsee counties.

Polygonum virginianum L. Common, in moist wooded canyons and floodplain woods. Found throughout the area.

Rumex acetosella L. Rare, in waste ground and cultivated fields. Reported for Pottawatomie, Riley and Wabaunsee counties by Gates (1940).

Rumex altissimus Wood. Common, in alluvial soil along streams, impoundments, in cultivated fields, waste ground and roadside ditches. Encountered throughout the area.

Rumex crispus L. Common, in cultivated fields, waste ground, along roadsides, railway right-of-ways, and margins of floodplain woods. Found throughout the area.

Rumex maritimus L. var. *fueginus* (Phil.) Dusen. Rare, in sandy soil along the Kansas River. Reported for Riley County by Gates (1940).

Rumex patientia L. Occasional, in waste ground, along roadsides and railway right-of-ways. Known from the northern part of the area.

Rumex stenophyllus Ledeb. Rare, in alluvial soil along the streams. Found only in the northern part of the area.

Rumex venosus Pursh. Rare, in prairies on sandy soils. Reported for Geary, Pottawatomie and Riley counties by Gates (1940).

CHENOPODIACEAE

Atriplex hortensis L. Rare, escapes from cultivation into waste places. Reported for Pottawatomie County by Gates (1940).

Chenopodium album L. Common, in waste places, cultivated fields, along roadsides and railroad right-of-ways. Found throughout the area.

Chenopodium ambroisoides L. Rare, in waste places around dwellings and along railroad right-of-ways. Reported from Morris, Pottawatomie and Riley counties.

Chenopodium berlandieri Moq. var. *boscianum* (Moq.) Vahl. Occasional, in alluvial woods, moist wooded canyons, and in moist waste places. Occurs throughout the area.

Chenopodium gigantospermum Aellen. Common, in floodplain woods and wooded canyons. Found throughout the area.

Chenopodium glaucum L. Rare, in floodplain woods and moist waste places. Found in Chase County.

Chenopodium leptophyllum Nutt. Occasional, in dry wooded canyons and waste places. Occurs throughout the area.

Chenopodium standleyanum Aellen. Occasional, in floodplain woods, along streambeds, and in moist waste places. Encountered throughout the area.

Cycloloma atriplicifolium (Spreng.) Coult. Rare, in sandy areas along streams and sandy waste places. Found in the northern part and in Cowley County along Arkansas River floodplain.

Kochia scoparia (L.) Schrader. Common, in waste places, along roadsides and railway right-of-ways. Found throughout the area.

Monolepis nuttalliana (Schult.) Green. Occasional, in waste ground, overgrazed prairies, along roadsides and railroad right-of-ways. Found throughout the area.

Salsola kali L. Occasional, in open waste places, along open floodplains, roadsides and railroad right-of-ways. Reported for Pottawatomie, Riley and Wabaunsee counties by Gates (1940).

AMARANTHACEAE

Amaranthus graecizans L. Common, in waste places, cultivated fields, along roadsides and railroad right-of-ways. Occurs throughout the area.

Amaranthus hybridus L. Common, in floodplain woods, and moist wooded canyons. Encountered throughout the area.

Amaranthus retroflexus L. Common, in waste places, cultivated fields and along roadsides. Found throughout the area.

Amaranthus spinosus L. Occasional, in waste places and cultivated fields. Found in Pottawatomie and Wabaunsee counties.

Amaranthus tamariscinus (Nutt.) Wood. Common, in waste places, cultivated fields, along roadsides and railroad right-of-ways. Encountered throughout the area.

Froelichia floridana (Nutt.) Moq. var. *campestris* (Small) Fern. Occasional, grows in sandy soil along streambeds. Known from Cowley, Morris, Pottawatomie and Riley counties.

Froelichia gracilis (Hook.) Moq. Occasional, grows in sandy soil along streambeds. Known from Geary, Pottawatomie and Riley counties.

Tidestromia lanuginosa (Nutt.) Standl. Rare, occurs in waste ground and along railway right-of-ways. Reported for Riley and Lyon counties by Gates (1940).

NYCTAGINACEAE

Mirabilis albida (Walt.) Heimerl. Occasional, in rocky upland prairies, on rocky prairie slopes, margins of wooded canyons and along rocky roadside embankments. Found in Cowley, Marshall, Morris, Riley and Wabaunsee counties.

Mirabilis linearis (Pursh.) Heimerl. Common, in rocky upland prairies, on rocky prairie slopes, margins of wooded canyons and along rocky roadsides. Occurs throughout the area.

Mirabilis nyctaginea (Michx.) MacM. Common, in moist rich soil along railway right-of-ways, roadside ditches, drainage areas, waste places and open floodplain woods. Encountered throughout the area.

PHYTOLACCACEAE

Phytolacca americana L. Common, in waste ground, farmyards, along roadsides and margins of wooded areas. Occurs throughout the area.

AIZOACEAE

Mollugo verticillata L. Common, along roadsides, railroad right-of-ways, in cultivated fields and waste places. Occurs throughout the area.

PORTULACACEAE

Claytonia virginica L. Occasional, in upland prairies, prairie canyons, open areas in wooded canyons and open floodplain woods. Known from Cowley County.

Portulaca mundula Johnston. Rare, in sandy soil. Reported for Riley County by Gates (1940).

Portulaca oleracea L. Occasional, in waste ground and cultivated fields. Occurs throughout the area.

CARYOPHYLLACEAE

Agrostemma githago L. Rare, introduced into cultivated fields and waste ground. Reported for Riley County by Gates (1940).

Arenaria serpyllifolia L. Rare, in sandy soil, cultivated fields and open waste places. Reported for Geary and Riley counties by Gates (1940).

Arenaria stricta Michx. var. *texana* Robins. Rare, on rocky prairie slopes, along prairie ravines and in low sandy areas. Reported for Cowley County by Gates (1940).

Cerastium brachypodum (Engelm.) Robins. Rare, in open wooded areas, overgrazed prairies, roadside ditches, cultivated fields and waste places. Known from Wabaunsee County.

Lychnis alba Mill. Rare, introduced into cultivated fields and waste places. Reported for Riley County by Gates (1940).

Saponaria officinalis L. Common, escapes cultivation and grows along roads, abandoned farmyards and in waste places. Encountered throughout the region.

Saponaria vaccaria L. Rare, introduced along roadsides, railroad right-of-ways and in waste places. Reported for Riley County by Gates (1940).

Silene antirrhina L. Common, along roadsides, railway right-of-ways in overgrazed prairies, cultivated fields and waste places. Occurs throughout the area.

Silene cucubalus Wibel. Rare, introduced into cultivated fields and waste places. Reported for Marion and Riley counties by Gates (1940).

Silene noctiflora L. Rare, introduced into cultivated fields and waste places. Reported for Riley County by Gates (1940).

Silene stellata (L.) Ait. Common, in floodplain woods and along the margins of rich wooded areas. Occurs throughout the area.

Spergula arvensis L. Rare, introduced into cultivated fields and waste places. Reported for Riley County by Gates (1940).

Stellaria media (L.) Cyrill. Common, in lawns, cultivated fields and other such waste places. Found throughout the area.

CERATOPHYLLACEAE

Ceratophyllum demersum L. Occasional, grows in shallow water of impoundments. Found in Chase and Riley counties.

NYMPHAEACEAE

Nelumbo lutea (Willd.) Pers. Rare, grows in impoundments. Known from Morris County.

Nuphar advena (Ait.) Ait. Rare, grows in impoundments. Known from Cowley County.

ANNONACEAE

Asimina triloba (L.) Dunal. Common, in stream valley woods. Found throughout the area except in Chase, Geary, Marion, Morris and Marshall counties.

RANUNCULACEAE

Anemone canadensis L. Occasional, in alluvial soil along wooded floodplains. Reported for Pottawatomie and Riley counties by Gates (1940).

Anemone caroliniana Walt. Occasional, in upland prairies and prairie canyons. Occurs throughout the area.

Anemone virginiana L. Occasional, in floodplain woods. Known from Marshall, Pottawatomie, Riley and Wabaunsee counties.

Aquilegia canadensis L. Occasional, on rocky wooded slopes and in rich lowland woods. Collected from Cowley and Marshall counties.

Clematis dioscoreifolia Levl. & Vaniot. Occasional, escapes from cultivation to along roadsides, railway right-of-ways and waste places. Known from Cowley County.

Clematis ligusticifolia Nutt. Rare, in wooded canyons. Reported for Geary and Cowley counties by Gates (1940).

Clematis pitcheri T. & G. Occasional, in wooded canyons and floodplain woods. Occurs throughout the area.

Clematis virginiana L. Occasional, in wooded canyons and floodplain woods. Reported for Marshall, Pottawatomie and Riley counties by Gates (1940).

Delphinium ajacis L. Occasional, escapes from cultivation to along roadsides and in waste places. Known from Marshall and Cowley counties.

Delphinium tricorne Michx. Occasional, in rich wooded canyons and in floodplain woods. Found throughout the area.

Delphinium virescens Nutt. Common, in upland prairies, prairie canyons, cultivated fields, along roadsides and railway right-of-ways. Occurs throughout the area.

Isopyrum biternatum (Raf.) T. & G. Rare, in moist wooded canyons. Reported for Riley County by Gates (1940).

Myosurus minimus L. Rare, in moist cultivated fields, low alluvial ground and low waste places. Known from Geary, Pottawatomie and Riley counties.

Ranunculus abortivus L. Common, in wet places in prairies, open areas in woodlands, along streambanks, drainage areas, roadside ditches and railroad right-of-ways. Found throughout the area.

Ranunculus acris L. Occasional, in cultivated fields and moist prairie hay meadows. Reported for Lyon, Pottawatomie and Riley counties by Gates (1940).

Ranunculus cymbalaria Pursh. Common, growing in wet soil along margins of impoundments and streams. Known from Riley County.

Ranunculus flabellaris Raf. Rare, grows in water of impoundments and slow-moving streams. Reported for Morris and Riley counties by Gates (1940).

Ranunculus longirostris Godron. Rare, grows in water of impoundments and slow-moving streams. Reported for Riley County by Gates (1940).

Ranunculus sceleratus L. Occasional, in wet prairie areas, open floodplain woods, cultivated fields, along roadsides and railway right-of-ways. Known from throughout the area.

Thalictrum dasycarpum Fisch. and Ave-Lall. Occasional, along margins of moist woods, in moist wooded canyons and floodplain woods. Occurs throughout the area.

BERBERIDACEAE

Podophyllum peltatum L. Rare, in stream valley woods. Reported for Pottawatomie and Riley counties by Gates (1940).

MENISPERMACEAE

Cocculus carolinus (L.) D.C. Occasional, on rocky wooded slopes and wooded canyons. Known from Cowley County.

Menispermum canadense L. Common, in wooded canyons and in stream valley woods. Found throughout the area.

PAPAVERACEAE

Argemone polyanthemos (Fedde) Ownb. Occasional, in rocky overgrazed prairies, rocky roadside embankments and along railroad right-of-ways. Occurs in Geary, Pottawatomie, Riley and Wabaunsee counties.

Papaver rhoeas L. Occasional, escapes into waste places and moist woods. Reported for Wabaunsee County by Gates (1940).

FUMARIACEAE

Corydalis micrantha (Engelm.) Gray. Occasional, in rich woods, low cultivated fields and shaded waste places. Known from Cowley, Geary, Riley and Wabaunsee counties.

Dicentra cucullaria (L.) Bernh. Occasional, in rich woods. Found in Cowley, Marshall, Riley and Wabaunsee counties.

CRUCIFERAE

Alliaria officinalis Andrz. Rare, in floodplain woods. Found in Riley and Wabaunsee counties.

Arabis canadensis L. Occasional, in floodplain woods and wooded canyons. Known from Marshall, Morris and Wabaunsee counties.

Arabis hirsuta (L.) Scop. Occasional, in stream valley woods and wooded canyons. Found in Marshall, Pottawatomie and Riley counties.

Barbarea vulgaris R. Br. Occasional, in cultivated fields, waste places, open floodplains and along roadsides. Found in Pottawatomie and Riley counties.

Berteroa incana (L.) DC. Rare, in waste places. Reported for Riley County by Gates (1940).

Brassica campestris L. Rare, cultivated fields and waste places. Reported for Morris, Pottawatomie, Riley and Wabaunsee counties by Gates (1940).

Brassica juncea (L.) Cross. Rare, in cultivated fields and waste places. Reported for Riley County by Gates (1940).

Brassica kaber (DC.) L. Occasional, in cultivated fields and waste places. Known from Chase, Geary, Marshall, Morris and Riley counties.

Brassica nigra (L.) Koch. Occasional, in cultivated fields and waste places. Found throughout the area.

Camelina microcarpa Andrz. Occasional, in cultivated fields, waste places and along roadsides. Found throughout the area.

Capsella bursa-pastoris (L.) Medic. Common, in lawns, cultivated fields, waste places and along roadsides. Occurs throughout the area.

Cardamine bulbosa (Schreb.) BSP. Rare, in wet woods and prairies. Reported for Pottawatomie County by Gates (1940).

Cardaria draba (L.) Desv. Occasional in waste places, along roadsides and railroad right-of-ways. Occurs throughout the area.

Conringia orientalis (L.) Dumont. Rare, in waste places, along roadsides and railroad right-of-ways. Reported for Geary, Pottawatomie, and Riley counties by Gates (1940).

Dentaria laciniata Muhl. Occasional, in rich floodplain woods and sometimes in wooded canyons. Found in Lyon, Riley and Wabaunsee counties.

Descurainia pinnata (Walt.) Britt. Common, in waste places, overgrazed prairies, along railroad right-of-ways and roadsides. Occurs throughout the area.

Descurainia sophia (L.) Webb. Occasional, in waste places, along roadsides and railway right-of-ways. Known from Butler, Cowley and Riley counties.

Draba brachycarpa Nutt. Rare, in rocky prairies, cultivated fields, along railroad right-of-ways and roadsides. Reported for Riley County by Gates (1940).

Draba cuneifolia Nutt. Occasional, in rocky prairies, along limestone escarpments, railroad right-of-ways, and roadsides. Encountered throughout the area.

Draba reptans (Lam.) Fern. Occasional in rocky prairies, cultivated fields, waste places, along railroad right-of-ways and roadsides. Found in Cowley, Lyon, Pottawatomie, Riley and Wabaunsee counties.

Eruca sativa Mill. Rare, introduced into waste places. Reported for Riley County by Gates (1940).

Erysimum asperum DC. Rare, in rocky prairies, along railway right-of-ways and roadsides. Reported for Riley County by Gates (1940).

Erysimum repandum L. Common, in waste places, cultivated fields, along railroad right-of-ways and roadsides. Found throughout the area.

Hesperis matronalis L. Occasional, introduced along roadsides and in waste places. Encountered throughout the area.

Iodanthus pinnatifidus (Michx.) Steud. Rare, in floodplain woods. Reported for Pottawatomie County by Gates (1940).

Lepidium campestre (L.) R. Br. Rare, in cultivated fields and waste places. Reported for Riley County by Gates (1940).

Lepidium densiflorum Schrader. Common, in overgrazed prairies, cultivated fields, waste places, along railway right-of-ways and roadsides. Occurs throughout the area.

Lepidium ramosissimum Nels. Rare, in waste places and cultivated fields. Reported for Riley County by Gates (1940).

Lepidium virginicum L. Occasional, in cultivated fields, overgrazed prairies, waste places, along railway right-of-ways and roadsides. Found throughout the area.

Nasturtium officinale R. Br. Common, along streams and spring seepage areas growing either in shallow water or in mud at the edge of the water. Occurs throughout the area.

Raphanus sativus L. Occasional, escapes from cultivation into waste places. Reported for Riley County by Gates (1940).

Rorippa islandica (Oeder) Borbas. Occasional, in wet alluvial soil along streams, drainage areas, impoundments and in low cultivated fields. Found in Butler, Cowley, Riley and Wabaunsee counties.

Rorippa sessiliflora (Nutt.) Hitchc. Common, in wet alluvial soil along streams, impoundments, in floodplain woods and low cultivated fields. Occurs throughout the area.

Rorippa sinuata (Nutt.) Hitchc. Common, along floodplains, in low cultivated fields, railway right-of-ways and roadsides. Known throughout the area.

Sisymbrium altissimum L. Occasional, in cultivated fields, waste places, along railway right-of-ways and roadsides. Found in Geary and Marshall counties.

Sisymbrium officinale (L.) Scop. Occasional, in cultivated fields, farmyards, waste places, along railroad right-of-ways and roadsides. Found in Marshall, Pottawatomie, Riley and Wabaunsee counties.

Thlaspi arvense L. Common, in cultivated fields, overgrazed prairies, waste places, along railroad right-of-ways and roadsides. Occurs throughout the area.

CAPPARIDACEAE

Cleome serrulata Pursh. Rare, in sandy soil along streams. Reported for Pottawatomie and Riley counties by Gates (1940).

Polanisia trachysperma T. &. G. Occasional, in sandy prairies, sandy areas along streams and in sandy roadside ditches. Known from Cowley, Pottawatomie and Riley counties.

CRASSULACEAE

Penthorum sedoides L. Common, along streambanks, impoundments, drainage areas and roadside ditches. Found throughout the area.

SAXIFRAGACEAE

Ribes missouriense Nutt. Common, in wooded canyons, along fence rows and wooded roadsides. Found throughout the area.

Ribes odoratum Wendl. Occasional, in wooded canyons and along fence rows. Known from Butler and Cowley counties.

PLATANACEAE

Platanus occidentalis L. Common, in floodplain woods and wooded canyons. Occurs throughout the area.

ROSACEAE

Agrimonia parviflora Ait. Rare, in low wet prairie areas, along margins of drainage areas, impoundments and streams. Known from Pottawatomie, Riley and Wabaunsee counties.

Agrimonia pubescens Wallr. Occasional, in wooded canyons and floodplain woods. Known from Geary, Marshall, Morris, Pottawatomie, Riley and Wabaunsee counties.

Crataegus mackenzii Sarg. Rare, in rocky wooded canyons. Known only from Wabaunsee County.

Crataegus mollis (T. & G.) Scheele. Occasional, in wooded stream valleys. Found in Chase, Lyon, Marshall and Riley counties.

Crataegus succulenta Link. Occasional, in rocky wooded canyons and floodplain woods. Known from Pottawatomie and Wabaunsee counties.

Fragaria virginiana Duchesne. Occasional to common, in upland prairies, on prairie slopes, in prairie canyons and in open areas of wooded canyons. Found throughout the area.

Geum canadense Jacq. Common, in rich wooded canyons in wooded stream valleys. Encountered throughout the area.

Potentilla arguta Pursh. Occasional, in upland prairies, prairie canyons and in prairie railway right-of-ways. Found in Lyon, Marshall and Pottawatomie counties.

Potentilla nicolletii (S. Wats.) Sheld. Rare, in low ground along streams. Reported for Riley County by Gates (1940).

Potentilla paradoxa Nutt. Rare, in wet alluvial soil along impoundments and streams. Reported for Riley County by Gates (1940).

Potentilla recta L. Occasional, in cultivated fields, prairie hay meadows, overgrazed prairies, waste ground, along roadsides and railroad right-of-ways. Found in Cowley, Lyon, Marshall, Riley and Wabaunsee counties.

Potentilla rivalis Nutt. Rare, in waste ground and alluvial soil along streams and impoundments. Reported for Riley County by Gates (1940).

Potentilla simplex Michx. Occasional, along margins of wooded areas and in rocky wooded canyons. Found in Pottawatomie and Wabaunsee counties.

Prunus americana Marsh. Occasional, in wooded fence rows, wooded canyons and sometimes overgrazed prairies. Encountered throughout the area.

Prunus hortulana Bailey. Occasional, in open wooded canyons, along borders of wooded areas and along streams. Found in Butler and Cowley counties.

Prunus mahaleb L. Rare, escapes from cultivation to along roadsides and wooded fence rows. Known from Lyon, Marshall, Riley and Wabaunsee counties.

Prunus mexicana S. Wats. Occasional, in rocky wooded canyons and along wooded roadsides. Found in Cowley, Geary, Marshall, Pottawatomie, Riley and Wabaunsee counties.

Prunus munsoniana Wight & Hedrick. Occasional along the margins of wooded areas and streams. Known from Butler and Cowley counties.

Prunus serotina Ehrh. Occasional, in wooded canyons and wooded areas along streams. Occurs in Riley and Wabaunsee counties.

Prunus virginiana L. Occasional, in wooded canyons and along streams. Occurs throughout the area.

Pyrus coronaria L. Rare, in low open woods along streams. Reported for Riley County by Gates (1940).

Pyrus ioensis (Wood.) Bailey. Occasional, in open areas in wooded areas, along margins of woods and wooded streambanks. Found in Marshall, Pottawatomie and Riley counties.

Rosa arkansas Porter var. *suffulta* (Greene) Cockerell. Common, in upland prairies on prairie slopes, along roadsides and railroad right-of-ways. Occurs throughout the area.

Rosa blanda Ait. Occasional, in open wooded areas and along roadsides. Found in Marshall, Pottawatomie and Riley counties.

Rosa multiflora Thunb. Occasional, planted along fence rows and roadsides, sometimes escaping into overgrazed prairies and open ground. Known from Butler, Cowley and Lyon counties.

Rubus allegheniensis Porter. Occasional, in wooded canyons. Found in Cowley County.

Rubus enslenii Tratt. Occasional, in upland prairies, on prairie slopes and along roadsides. Known from Pottawatomie and Wabaunsee counties.

Rubus flagellaris L. Occasional, in rocky wooded canyons and along wooded roadsides. Found in Cowley, Morris, Pottawatomie and Riley counties.

Rubus occidentalis L. Occasional to common, in rocky wooded canyons. Found throughout the area.

Rubus orarius Blanchard. Rare, in open wooded areas, along margins of woods and roadsides. Collected once by H. A. Stephens in Wabaunsee County.

Rubus ostryifolius Rydb. Occasional to common, in wooded canyons, on prairie slopes, along roadsides and railway right-of-ways. Found throughout the area.

LEGUMINOSAE

Acacia angustissima (Mill.) Ktze. Rare, in rocky upland prairies and occasionally along the roadsides. Known from Cowley County.

Amorpha canescens Pursh. Common to abundant, in upland prairies, prairie hay meadows, prairie canyons and sometimes in open wooded canyons. Occurs throughout the area.

Amorpha fruticosa L. Common, along streams, drainage areas, impoundments, and along margins of stream valley woods. Found throughout the area.

Amorpha nana Nutt. Rare, in rocky upland prairies and on rocky prairie slopes. Known from Chase, Pottawatomie, Riley and Wabaunsee counties.

Amphicarpa bracteata (L.) Fern. Occasional, in wooded canyons and floodplain woods. Found throughout the area.

Apios americana Medic. Rare, in floodplain woods. Known from Cowley, Marshall, Pottawatomie and Riley counties.

Astragalus canadensis L. Occasional, in rocky or open lowland area, margins of canyon and floodplain woods. Found in Cowley, Geary, Marshall, Morris, Pottawatomie and Riley counties.

Astragalus caryocarpus Ker. Common, in rocky upland prairies, on rocky prairie slopes, in open canyon woods, along railroad right-of-ways and roadsides. Occurs throughout the area.

Astragalus lotiflorus Hook. Occasional, in rocky upland prairies and on rocky prairie slopes. Occurs in Geary, Pottawatomie, Riley and Wabaunsee counties.

Astragalus plattensis Nutt. Occasional, in rocky upland prairies and on rocky prairie slopes. Found in Geary, Lyon, Riley and Wabaunsee counties.

Baptisia australis (L.) R. Br. var. *minor* (Lehm.) Fern. Common, in rocky upland prairies, prairie hay meadows and prairie canyons. Occurs throughout the area.

Baptisia leucantha T. & G. Occasional, in upland prairies, prairie hay meadows, prairie canyons and in alluvial soil along streams. Collected from Lyon and Wabaunsee counties.

Baptisia leucophaea Nutt. Common, in rocky upland prairies and prairie hay meadows. Encountered throughout the area.

Cassia fasciculata Michx. Common, in rocky upland prairies, on rocky prairie slopes, along railway right-of-ways and roadsides. Found throughout the area.

Cassia marilandica L. Occasional, in open rocky woods, on rocky prairie slopes, in rocky upland prairies, alluvial soil along roadsides and drainage areas. Occurs throughout the area.

Cercis canadensis L. Common, in open canyon woods, along the margins of lowland, floodplain woods and along open rocky streambanks. Found throughout the area.

Coronilla varia L. Occasional, in waste places and often planted along roadside embankments. Known from Geary, Marshall and Wabaunsee counties.

Crotalaria sagittalis L. Rare, in prairies, on open wooded slopes, in waste places and along roadsides. Reported for Morris, Pottawatomie, and Riley counties by Gates (1940).

Dalea alopecuroides Willd. Rare, in prairies on sandy soil and along rivers. Reported for Pottawatomie, Riley and Wabaunsee counties by Gates (1940).

Dalea aurea Nutt. Occasional, in rocky upland prairies, on rocky prairie slopes and along rocky roadsides. Occurs throughout the area.

Dalea enneandra Nutt. Rare, in rocky upland prairies and along roadsides. Known from Cowley, Pottawatomie and Riley counties.

Desmanthus illinoensis (Michx.) MacMill. Common, in rocky upland prairies, on rocky prairie slopes, in open wooded canyons, along railway right-of-ways and roadsides. Found throughout the area.

Desmodium canadense (L.) DC. Occasional, in moist upland prairies, moist prairie hay meadows and prairie canyons. Found throughout the area.

Desmodium canescens (L.) DC. Occasional, in wooded canyons and in alluvial soil along streams. Known from Chase, Geary, Marshall, Morris, Pottawatomie, Riley and Wabaunsee counties.

Desmodium cuspidatum (Muhl.) Loud. Occasional, in rocky wooded canyons. Known from Geary, Lyon, Morris and Riley counties.

Desmodium glutinosum (Muhl.) Wood. Common, in rocky wooded canyons and in floodplain woods. Occurs throughout the area.

Desmodium illinoense Gray. Common, in rocky upland prairies, on rocky prairie slopes and in prairie canyons. Encountered throughout the area.

Desmodium paniculatum (L.) DC. Rare, in wooded canyons and moist woods along streams. Known from Cowley County.

Desmodium sessilifolium (Torr.) T. & G. Common, in upland prairies, on rocky prairie slopes and in prairie canyons. Found throughout the area.

Gleditsia triacanthos L. Common, in floodplain woods and in wooded canyons. Occurs throughout the area.

Glycyrrhiza lepidota Pursh. Common, in overgrazed upland prairies, prairie hay meadows, prairie canyons, along railway right-of-ways and roadsides. Found throughout the region.

Gymnocladus dioica (L.) K. Koch. Common, in floodplain woods. Occurs throughout the area.

Lespedeza capitata Michx. Common, in upland prairies, on rocky prairie slopes, on open wooded slopes, in prairie canyons along railway right-of-ways and roadsides. Found throughout the area.

Lespedeza cuneata (Dumont) G. Don. Rare, in upland prairies and along roadsides. Collected from Butler County.

Lespedeza intermedia (S. Wats.) Britt. Rare, in open wooded canyons. Known from Butler County.

Lespedeza nuttallii Darl. Rare, in open wooded canyons. Known from Chase County.

Lespedeza repens (L.) Bart. Occasional, in open wooded canyons. Occurs in Geary, Pottawatomie and Riley counties.

Lespedeza stipulacea Maxin. Common, along roadsides, railroad right-of-ways and planted in overgrazed prairies. Found throughout the area.

Lespedeza striata (Thunb.) H. & A. Rare, in open, wooded canyons and along roadsides. Known from Cowley and Pottawatomie counties.

Lespedeza violacea (L.) Pers. Occasional, in open rocky woods and in rocky prairies. Occurs in Geary, Pottawatomie, Riley and Wabaunsee counties.

Lespedeza virginica (L.) Britt. Occasional, in open rocky woods. Found in Cowley County.

Lotus corniculatus L. Occasional, in waste ground, along roadsides and sometimes planted in overgrazed prairies. Known from Pottawatomie County.

Lotus purshianus Clements & Clements. Occasional, in upland prairies, on rocky prairie slopes and along roadsides. Found in Marshall County.

Medicago lupulina L. Occasional, in lawns, cultivated fields, waste ground, overgrazed prairies, along roadsides and railroad right-of-ways. Found throughout the area.

Medicago sativa L. Common, cultivated for hay and escapes into waste ground, roadsides and railway right-of-ways. Occurs throughout the area.

Melilotus alba Desr. Common, along roadsides, railway right-of-ways, in cultivated fields and other waste places. Encountered throughout the area.

Melilotus officinalis (L.) Desr. Common to abundant, along roadsides, railroad right-of-ways, in cultivated fields and other waste places. Occurs throughout the area.

Oxytropis lambertii Pursh. Rare, in upland prairies and on rocky, prairie slopes. Known from Geary and Riley counties.

Petalostemon candidum (Willd.) Michx. Common, in rocky upland prairies, on rocky prairie slopes, in prairie canyons, along railroad right-of-ways and roadsides. Found throughout the area.

Petalostemon multiflorum Nutt. Common, in rocky upland prairies, on rocky prairie slopes, along railway right-of-ways and roadsides. Occurs throughout the area.

Petalostemon purpureum (Vent.) Rydb. Common, in rocky upland prairies, on rocky prairie slopes, in prairie canyons, along railroad right-of-ways and roadsides. Encountered throughout the area.

Psoralea argophylla Pursh. Occasional, in upland prairies, prairie hay meadows and in prairie canyons. Occurs throughout the area.

Psoralea esculenta Pursh. Occasional, in upland prairies, prairie hay meadows and prairie canyons. Found throughout the area.

Psoralea lanceolata Pursh. Rare, in sandy, prairie areas. Known from Geary and Riley counties.

Psoralea tenuiflora Pursh. var. *floribunda* (Nutt.) Rydb. Common, in upland prairies, prairie hay meadows and prairie canyons. Occurs throughout the area.

Psoralea tenuiflora Pursh. var. *tenuiflora.* Common, in upland prairies, prairie hay meadows and prairie canyons. Found throughout the area.

Robinia pseudo-acacia L. Occasional, on rocky wooded slopes, in open floodplain woods and waste ground. Found in Cowley, Geary, Lyon, Marshall, Morris, Pottawatomie, Riley and Wabaunsee counties.

Schrankia uncinata Willd. Common, in rocky upland prairies, on rocky prairie slopes, along railway right-of-ways and roadsides. Occurs throughout the area.

Sesbania exaltata (Raf.) Cory. Rare, reported as escaped from cultivation in Riley County by Gates (1940).

Strophostyles helvola (L.) Ell. Occasional, in rocky wooded canyons and floodplain woods. Known from Lyon, Marshall, Pottawatomie and Riley counties.

Strophostyles leiosperma (T. & G.) Piper. Occasional, in rocky upland prairies, on rocky prairie slopes, cultivated fields, waste ground, along railway right-of-ways and roadside embankments. Known from Cowley, Geary, Marshall, Pottawatomie, Riley and Wabaunsee counties.

Tephrosia virginiana (L.) Pers. Occasional, in open wooded canyons. Reported for Riley and Pottawatomie counties by Gates (1940).

Trifolium hybridum L. Occasional, in abandoned fields, overgrazed prairies, waste ground, along railway right-of-ways and roadsides. Found in Cowley and Riley counties.

Trifolium pratense L. Common, in cultivated fields, overgrazed prairies, waste ground, along railway right-of-ways and roadsides. Found throughout the area.

Trifolium procumbens L. Occasional, in cultivated fields, prairies, open woodlands, along railway right-of-ways and roadsides. Known from Cowley County.

Trifolium repens L. Common, in cultivated fields, overgrazed prairies, along railway right-of-ways and roadsides. Found throughout the region.

Vicia americana Muhl. Occasional, in open woods and thickets. Found throughout the area.

Vicia sparsifolia Nutt. Occasional, in overgrazed prairies, waste ground, and along roadsides. Known from Pottawatomie County.

Vicia villosa Roth. Occasional, in cultivated fields, overgrazed prairies, waste ground and along roadsides. Known from Cowley and Riley counties.

OXALIDACEAE

Oxalis dillenii Jacq. Common, in cultivated fields, rocky prairies, open wooded areas, along railroad right-of-ways and roadsides. Throughout the area.

Oxalis stricta L. Common, in wooded canyons, wooded floodplains, cultivated fields, waste ground, along railroad right-of-ways and roadsides. Occurs throughout the region.

Oxalis violacea L. Common, in open wooded canyons, cultivated fields, rocky upland prairies and along roadsides. Encountered throughout the area.

GERANIACEAE

Erodium cicutarium L'Her. Rare, in waste places, cultivated fields and along margins of impoundments. Found in Chase and Geary counties.

Geranium carolinianum L. Common, in cultivated fields, waste places, overgrazed prairies, prairie hay meadows, along roadsides and railway right-of-ways. Throughout the area.

LINACEAE

Linum sulcatum Riddell. Common, in upland prairies, prairie hay meadows and prairie canyons. Occurs throughout the area.

Linum usitatissimum L. Occasional, along roadsides, railway right-of-ways and in waste places. Known from Cowley, Marshall and Riley counties.

ZYGOPHYLLACEAE

Tribulus terrestris L. Common, in cultivated fields, waste ground, severely overgrazed prairies, along roadsides and railroad right-of-ways. Occurs throughout the area.

RUTACEAE

Ptelea trifoliata L. Occasional, along margins of wooded canyons, in wooded canyons and stream valley woods. Collected in Cowley County and reported for Riley County by Gates (1940).

Zanthoxylum americanum Mill. Occasional, in wooded canyons. Encountered throughout the area.

SIMARUBACEAE

Ailanthus altissima (Mill.) Swingle. Occasional, escapes from cultivation to waste ground and along roadsides. Known from Butler, Geary, Riley and Wabaunsee counties.

POLYGALACEAE

Polygala incarnata L. Rare, in sandy soils of prairie areas. Reported for Pottawatomie County by Gates (1940).

Polygala verticillata L. Common, in open wooded canyons, on rocky prairie slopes and in rocky upland prairies. Known from Cowley, Geary, Pottawatomie, Riley and Wabaunsee counties.

EUPHORBIACEAE

Acalypha gracilens Gray. Occasional, in rocky upland prairies, on rocky prairie slopes, in open wooded canyons. Occurs throughout the area.

Acalypha ostryaefolia Riddell. Common, in floodplain woods and in low cultivated ground. Found throughout the area.

Acalypha rhomboidea Raf. Occasional, in alluvial soil along drainage areas and streams. Reported for Riley County by Gates (1940).

Acalypha virginica L. Common, in upland prairies, prairie canyons, open wooded canyons, cultivated fields, along railroad right-of-ways and roadsides. Occurs throughout the area.

Croton capitatus Michx. Common, in overgrazed upland prairies, cultivated fields, waste places, along railway right-of-ways and roadsides. Found throughout the area.

Croton glandulosus L. Rare, in upland prairies, open wooded canyons, cultivated fields, waste places, along railway right-of-ways and roadsides. Known from Cowley County.

Croton monanthogynous Michx. Common, in rocky upland prairies, along limestone escarpments on rocky slopes and along roadside embankments. Encountered throughout the area.

Croton texensis (Klotzsch) Muell. Arg. Rare, in sandy prairies, alluvial soil along streams, along railway right-of-ways and roadsides. Reported for Riley County by Gates (1940).

Ditaxis mercurialina (Nutt.) Coult. Occasional, in rocky upland prairies and on rocky prairie slopes. Found in Butler, Chase and Cowley counties.

Euphorbia commutata Engelm. Rare, in rocky wooded canyons and in floodplain woods. Reported for Geary County by Gates (1940).

Euphorbia corollata L. Common, in upland prairies, prairie canyons, open wooded canyons, along railway right-of-ways and roadsides. Found throughout the area.

Euphorbia cyparissias L. Occasional, planted in cemeteries and occasionally escaping into cultivated fields and roadsides. Known from Pottawatomie, Riley and Wabaunsee counties.

Euphorbia dentata Michx. Common, in wooded canyons, overgrazed prairies, cultivated fields, waste places, along railway right-of-ways and roadsides. Encountered throughout the area.

Euphorbia glyptosperma Engelm. Common, in prairie canyons, in alluvial soil along streams and low waste places. Occurs throughout the area.

Euphorbia heterophylla L. Common, in wooded canyons and floodplain woods and along wooded drainage areas. Known throughout the area.

Euphorbia hexagona Nutt. Occasional, in alluvial soil along streams. Known from Cowley, Geary, Pottawatomie, Riley and Wabaunsee counties.

Euphorbia humistrata Engelm. Rare, in alluvial soil along streams and impoundments. Reported for Geary County by Gates (1940).

Euphorbia maculata L. Common, in cultivated fields, waste places, along railroad right-of-ways and roadsides. Found throughout the area.

Euphorbia marginata Pursh. Common, in cultivated fields, overgrazed prairies, waste places, along railway right-of-ways and roadsides. Found throughout the area.

Euphorbia missurica Raf. Common, on rocky prairie slopes along limestone escarpments and in rocky upland prairies. Occurs throughout the area.

Euphorbia nutans Lag. Common, in cultivated fields, waste places, open floodplain woods along railway right-of-ways and roadsides. Found throughout the area.

Euphorbia podperae Croiz. Rare, in cultivated fields, waste places, along railway right-of-ways and roadsides. Known from Marion and Marshall counties.

Euphorbia prostrata Ait. Occasional, in overgrazed prairies, waste places, along railway right-of-ways and roadsides. Found throughout the area.

Euphorbia serpens HBK. Common, in open alluvial soil along streams, drainage areas and impoundments. Occurs throughout the area.

Euphorbia spathulata Lam. Common, in rocky upland prairies, on rocky prairie slopes, in wooded canyons and in roadside ditches. Occurs throughout the area.

Euphorbia stictospora Engelm. Common, in overgrazed prairies, cultivated fields, waste places, along railway right-of-ways and roadsides. Encountered throughout the area.

Tragia betonicifolia Nutt. Occasional, in overgrazed prairies, on rocky prairie slopes and in roadside ditches. Found throughout the area.

Tragia ramosa Torr. Rare, in overgrazed prairies, on rocky prairie slopes and in roadside ditches. Occurs throughout the area.

CALLITRICHACEAE

Callitriche heterophylla Pursh. Rare, grows either in the water or at the edge of streams, springs and impoundments. Reported for Riley County by Gates (1940).

ANACARDIACEAE

Rhus aromatica Ait. Abundant, on limestone escarpments and on prairie slopes. Occurs throughout the area.

Rhus copallina L. Rare, in prairies and along margins of wooded areas. Known from Cowley and Riley counties.

Rhus glabra L. Abundant, in upland prairies and along the margins of wooded areas. Found throughout the area.

Rhus radicans L. Common, in floodplain woods, on rocky wooded slopes, along roadsides, fence rows and railroad right-of-ways. Found throughout the area.

CELASTRACEAE

Celastrus scandens L. Common, in alluvial woods, wooded canyons, on wooded slopes and along fence rows. Encountered throughout the area.

Euonymus atropurpureus Jacq. Common, in alluvial woods, wooded canyons and on wooded slopes. Found throughout the area.

STAPHYLEACEAE

Staphylea trifolia L. Occasional, in wooded canyons. Known from Cowley, Geary, Pottawatomie, Riley and Wabaunsee counties.

ACERACEAE

Acer negundo L. Common, in floodplain woods and wooded canyons. Found throughout the area.

Acer saccharinum L. Common, in floodplain woods and wooded canyons. Occurs throughout the area.

HIPPOCASTANACEAE

Aesculus glabra Willd. Common, in wooded areas along streams and drainage areas. Encountered throughout the area.

SAPINDACEAE

Sapindus drummondii Hook. & Arn. Occasional, along the margins of wooded areas developed on rocky slopes and sometimes in low areas along streams. Found in Chase, Cowley, Geary and Riley counties.

BALSAMINACEAE

Impatiens capensis Meerb. Rare, in alluvial woods and along streambanks. Reported for Pottawatomie and Wabaunsee counties by Gates (1940).

Impatiens pallida Nutt. Rare, in alluvial woods and along streambanks. Reported for Riley County by Gates (1940).

RHAMNACEAE

Ceanothus americanus L. Occasional, on rocky prairie slopes and in open areas of wooded canyons. Occurs throughout the area.

Ceanothus ovatus Desf. Common, on rocky prairie slopes. Occurs throughout the area.

Rhamnus lanceolata Pursh. Occasional, in open wooded canyons and open floodplain woods. Found in the northern part of the area.

VITACEAE

Ampelopsis cordata Michx. Occasional, in rich stream valley woods. Occurs in Cowley, Geary, Pottawatomie, Riley and Wabaunsee counties.

Parthenocissus quinquefolia (L.) Planch. Common, in rocky wooded canyons and rich stream valley woods. Found throughout the area.

Parthenocissus vitacea (Knerr.) Hitchc. Occasional, in rocky wooded canyons and rich stream valley woods. Known from Chase, Geary, Morris, Pottawatomie, Riley and Wabaunsee counties.

Vitis aestivalis Michx. Rare, in rocky wooded canyons and rich stream valley woods. Found in Chase and Cowley counties.

Vitis cinera Engelm. Occasional, in rocky wooded canyons and rich stream valley woods. Occurs in Butler, Cowley, Pottawatomie, Riley and Wabaunsee counties.

Vitis riparia Michx. Occasional, in rocky wooded canyons and rich stream valley woods. Found throughout the area.

Vitis vulpina L. Common, in rocky wooded canyons and rich stream valley woods. Occurs throughout the area.

TILIACEAE

Tilia americana L. Occasional, in rich wooded canyons and in wooded areas along streams. Known from Geary, Lyon, Marshall, Pottawatomie, Riley and Wabaunsee counties.

MALVACEAE

Abutilon theophrasti Medic. Common, in cultivated fields, waste places, overgrazed prairies, along railroad right-of-ways and roadsides. Occurs throughout the area.

Callirhoe alcaeoides (Michx.) Gray. Common, in upland prairies, prairie hay meadows and in prairie canyons. Found throughout the region.

Callirhoe involucrata (T. & G.) Gray. Occasional, along roadsides, railway right-of-ways and sometimes in overgrazed prairies. Encountered throughout the region.

Hibiscus militaris Cav. Occasional, along streambanks, impoundments and drainage areas. Reported for Pottawatomie, Riley and Wabaunsee counties by Gates (1940).

Hibiscus trionum L. Common to abundant, in cultivated fields, waste places, along roadsides and railroad right-of-ways. Occurs throughout the area.

Malva neglecta Wallr. Occasional, in cultivated fields, waste ground, along railway right-of-ways and roadsides. Found throughout the area.

Malva rotundifolia L. Occasional, in cultivated fields, waste ground, along railway right-of-ways and roadsides. Known from Cowley, Geary, Pottawatomie and Riley counties.

Sida spinosa L. Common, in cultivated fields, overgrazed prairies, along railroad right-of-ways and roadsides. Occurs throughout the area.

Sphaeralcea angusta (Gray.) Fern. Rare, in rocky prairies, along rocky streambeds and rocky roadside ditches. Known from Chase, Geary, Pottawatomie and Riley counties.

Sphaeralcea coccinea (Pursh.) Rydb. Rare, in rocky prairie areas. Known from Cowley and Riley counties.

HYPERICACEAE

Hypericum mutilum L. Occasional, in moist places in upland prairies, along margins of drainage areas and impoundments. Reported for Pottawatomie and Riley counties by Gates (1940).

Hypericum perforatum L. Occasional, in rocky upland prairies, waste places, along railway right-of-ways and roadsides. Found in Chase, Marshall, Pottawatomie and Riley counties.

Hypericum punctatum L. Occasional, in cultivated fields, waste places, along railroad right-of-ways, roadsides and in open wooded areas. Known from Marshall, Pottawatomie and Riley counties.

Hypericum sphaerocarpon Michx. Occasional, in rocky prairies, drainage ravines, and open wooded areas. Known from Lyon, Pottawatomie and Wabaunsee counties.

ELATINACEAE

Bergia texana (Hook.) Seubert. Rare, in sandy or alluvial soil. Reported for Pottawatomie County by Gates (1940).

CISTACEAE

Helianthemum bicknellii Fern. Rare, in rocky, prairie areas and in dry, open woods. Reported for Pottawatomie and Riley counties by Gates (1940).

Lechea tenuifolia Michx. Rare, in rocky, open, wooded areas. Reported for Pottawatomie County by Gates (1940).

VIOLACEAE

Hybanthus verticillatus (Ortega) Baill. Occasional, in rocky upland prairies and on rocky prairie slopes. Found throughout the area.

Viola bicolor Pursh. Common, in upland prairies, prairie hay meadows, along roadsides and railway right-of-ways. Found throughout the area.

Viola eriocarpa Schw. Occasional, in rocky wooded canyons and wooded stream valleys. Found in Cowley, Lyon and Wabaunsee counties.

Viola missouriensis Greene. Occasional, in wooded canyons and wooded stream valleys. Known from Cowley, Geary, Lyon and Riley counties.

Viola papilionacea Pursh. Occasional, in wooded canyons and wooded stream valleys. Found throughout the area.

Viola pedatifida G. Don. Occasional, in upland prairies, on prairie slopes, along roadside embankments and railway right-of-ways. Occurs in Cowley, Geary, Marshall, Morris, Pottawatomie and Riley counties.

Viola sororia Willd. Occasional, in wooded canyons and wooded stream valleys. Found in Geary, Riley and Wabaunsee counties.

LOASACEAE

Mentzelia oligosperma Nutt. Common, on rocky prairie slopes and rocky, roadside embankments. Occurs throughout the region.

CACTACEAE

Opuntia compressa (Salisb.) Macbr. Common, in overgrazed upland prairies and on rocky prairie slopes. Found throughout the area.

Mammillaria missouriensis Swett. Occasional, in upland prairies. Known from Chase, Riley and Waubaunsee counties.

Mammillaria viviparia (Nutt.) Haw. Rare, in upland prairies. Known from Marion County.

ELAEAGNACEAE

Elaeagnus angustifolia L. Occasional, planted around farmyards and escaping to roadsides and other waste ground. Occurs throughout the area.

LYTHRACEAE

Ammannia auriculata Willd. Rare, on muddy margins of impoundments, streams, drainage areas and roadside ditches. Known from Cowley and Riley counties.

Ammannia coccinea Rottb. Common, on muddy margins of impoundments, streams, drainage areas and roadside ditches. Found throughout the area.

Lythrum alatum Pursh. Common, in wet prairie areas, along drainage areas, impoundments, streambanks and roadside ditches. Found throughout the area.

ONAGRACEAE

Circaea quadrisulcata (Maxim.) Franch. & Sav. Occasional, in rich floodplain woods. Known from Marshall, Pottawatomie and Riley counties.

Epilobium coloratum Biehler. Occasional, in wet ground along streams, impoundments and low places. Known from Pottawatomie and Riley counties.

Epilobium leptophyllum Raf. Rare, in wet ground along streams, impoundments and low places. Reported for Riley County by Gates (1940).

Gaura coccinea Pursh. Rare, in overgrazed prairies, along roadsides and railway right-of-ways. Known from Geary and Riley counties.

Gaura filiformis Small. Common, in rocky upland prairies, along roadsides and railroad right-of-ways. Found throughout the region.

Jussiaea repens L. Occasional, in shallow water and on muddy margins of impoundments. Occurs throughout the area.

Ludwigia alternifolia L. Rare, in low wet places, along the margins of impoundments and streams. Known from Butler and Cowley counties.

Oenothera biennis L. Occasional, in cultivated fields, waste places, overgrazed prairies, along railroad right-of-ways and roadsides. Occurs throughout the area.

Oenothera laciniata Hill. Occasional, in cultivated fields, waste ground, prairie canyons, along railroad right-of-ways and roadsides. Occurs throughout the area.

Oenothera missouriensis Sims. Common, in rocky upland prairies, on rocky prairie slopes and along rocky roadside embankments. Occurs throughout the area.

Oenothera rhombipetala Nutt. Rare, in sandy prairies. Reported for Riley County by Gates (1940).

Oenothera serrulata Nutt. Common, in upland prairies, on prairie slopes, along railroad right-of-ways and roadsides. Encountered throughout the area.

Oenothera speciosa Nutt. Common to abundant, in overgrazed prairies, cultivated fields, waste places, along railway right-of-ways and roadsides. Found throughout the area.

Oenothera triloba Nutt. Occasional, in upland prairies, on prairie slopes and along roadsides. Known from Cowley County.

Stenosiphon linifolius (Nutt.) Britt. Common, on rocky prairie slopes and roadside embankments. Occurs throughout the area.

HALORAGIDACEAE

Myriophyllum heterophyllum Michx. Occasional, in impoundments and slow-moving streams. Reported for Riley County by Gates (1940).

Myriophyllum pinnatum (Walt.) BSP. Occasional in impoundments and slow-moving streams. Known from Chase, Morris and Riley counties.

UMBELLIFERAE

Berula pusilla (Nutt.) Fern. Rare, along low wet areas and spring seepage areas. Reported for Pottawatomie County by Gates (1940).

Chaerophyllum procumbens (L.) Crantz. var. *procumbens*. Occasional, in rocky wooded canyons and wooded stream valleys. Found in Chase, Cowley, Riley and Wabaunsee counties.

Chaerophyllum tainturieri Hook. var. *tainturieri*. Rare, in rocky wooded canyons and wooded stream valleys. Known in Pottawatomie and Wabaunsee counties.

Chaerophyllum texanum Coult. and Rose. Occasional, in rocky upland prairies, along roadsides and railroad right-of-ways. Occurs throughout the area.

Cicuta maculata L. var. *maculata*. Occasional, along prairie drainage areas, spring seepage areas, roadside ditches, margins of impoundments and streams. Occurs throughout the area.

Conium maculatum L. Common, in lowland cultivated fields, waste ground, fence rows, roadside ditches and railroad right-of-ways. Found throughout the area.

Cryptotaenia canadensis (L.) DC. Rare, in rocky wooded canyons and wooded stream valleys. Reported for Marshall, Riley and Pottawatomie counties by Gates (1940).

Daucus carota L. Rare, in cultivated fields, waste ground and along roadsides. Known from Morris, Pottawatomie and Riley counties.

Eryngium leavenworthii T. & G. Occasional to common, on rocky prairie slopes along rocky roadside embankments and rocky railroad right-of-ways. Found in Butler, Cowley, Chase, Marion, Morris and Geary counties.

Eryngium yuccifolium Michx. Occasional in moist prairie hay meadows and in prairie canyons. Found only in Butler County.

Falcaria sioides (Wibel) Aschers. Rare, in waste places and along roadsides. Reported for Mashall County by Gates (1940).

Lomatium foeniculaceum (Nutt.) Coult. & Rose. Common, in rocky upland prairies and on rocky prairie slopes. Found throughout the area.

Osmorhiza longistylis (Torr.) DC. Occasional, in wooded canyons and rich stream valley woods. Found in Cowley, Pottawatomie, Riley and Wabaunsee counties.

Polytaenia nuttallii DC. Common, in upland prairies, prairie hay meadows and prairie canyons. Found throughout the area.

Sanicula canadensis L. Common, in rocky wooded canyons and wooded stream valleys. Found throughout the area.

Sanicula gregaria Bicknell. Occasional, in rocky wooded canyons and wooded stream valleys. Known from Lyon and Riley counties.

Sanicula marilandica L. Occasional, in rocky wooded canyons and wooded stream valleys. Occurs in Lyon, Marshall, Riley and Wabaunsee counties.

Spermolepis inermis (Nutt.) Math. & Const. Occasional, in upland prairies, prairie hay meadows, along roadsides and railroad right-of-ways. Found throughout the area.

Thaspium trifoliatum (L.) Gray. Rare, in wooded canyons and rich stream valley woods. Reported for Wabaunsee County by Gates (1940).

Zizia aurea (L.) Koch. Occasional, in rocky wooded canyons and rich river valley woods. Occurs throughout the area.

CORNACEAE

Cornus amomum Mill. Rare, on rocky prairie slopes, in wooded canyons and along margins of floodplain woods. Known from Marshall County.

Cornus drummondii C. A. Meyer. Common, grows in dense stands along limestone escarpments on rocky slopes, in wooded canyons and along the margins of floodplain woods. Occurs throughout the area.

Cornus obliqua Raf. Rare, grows along limestone escarpment on rocky slopes. Known from Morris County.

PRIMULACEAE

Anagallis arvensis L. Rare, in cultivated fields and waste places. Reported from Lyon and Riley counties by Gates (1940).

Androsace occidentalis Pursh. Occasional, in cultivated fields, rocky upland prairies and open areas in wooded canyons. Found in Cowley, Marshall, Pottawatomie, Riley and Wabaunsee counties.

Lysimachia ciliata L. Occasional, in low wet prairie areas, floodplain woods, along impoundments and streams. Found in Butler, Geary, Morris, Pottawatomie, Riley and Wabaunsee counties.

SAPOTACEAE

Bumelia lanuginosa (Michx.) Pers. Occasional, in wooded canyons. Known from Cowley County.

EBENACEAE

Diospyros virginiana L. Occasional, along margins of floodplain woods, in wooded canyons and sometimes as scattered trees in prairie areas. Grows as a native in Cowley County and is cultivated in Riley County.

OLEACEAE

Fraxinus americana L. Occasional, in floodplain woods. Found in Butler, Marshall, Morris, Riley and Wabaunsee counties.

Fraxinus pennsylvanica Marsh var. *subintegerrima* (Vahl.) Fern. Common, in floodplain woods. Occurs throughout the area.

GENTIANACEAE

Gentiana puberulenta Pringle. Occasional, in well-managed upland prairies, on prairie slopes and in prairie canyons. Found in Geary, Marshall, Morris, Pottawatomie, Riley and Wabaunsee counties.

APOCYNACEAE

Apocynum cannabinum L. Common, in prairies, open wooded areas on rocky slopes, roadsides and waste places. Occurs throughout the area.

Apocynum sibiricum Jacq. Occasional, in prairie canyons, wet upland prairie areas and in alluvial soil along streambanks. Known throughout the area.

ASCLEPIADACEAE

Asclepias amplexicaulis Sm. Occasional, in upland prairies, open wooded areas on rocky slopes and along roadsides. Reported for Geary, Pottawatomie, Riley and Wabaunsee counties by Gates (1940).

Asclepias asperula (Dcne.) Woodson, spp. *capricorn* (Woodson) Woodson. Occasional, in upland prairies and on rocky, prairie slopes. Known from Butler and Cowley counties.

Asclepias incarnata L. Occasional, along the margins of streams and man-made impoundments. Found in Cowley, Marshall, Pottawatomie and Riley counties.

Asclepias lanuginosa Nutt. Rare, in prairie areas. Reported for Riley and Wabaunsee counties by Gates (1940).

Asclepias speciosa Torr. Rare, in prairie canyons. Reported for Geary, Pottawatomie and Riley counties by Gates (1940).

Asclepias stenophylla Gray. Common, in upland prairies, on rocky prairie slopes and in prairie canyons. Found throughout the area.

Asclepias sullivantii Engelm. Occasional, in moist upland prairies, prairie hay meadows and in prairie canyons. Known throughout the area.

Asclepias syriaca L. Common, along roadsides, railway right-of-ways, in overgrazed prairies, and in open wooded areas. Occurs throughout the area.

Asclepias tuberosa L. Common, in upland prairies, prairie hay meadows, and in prairie canyons. Encountered throughout the area.

Asclepias verticillata L. Common, in rocky upland prairies, on rocky prairie slopes, open wooded slopes, along roadsides and railway right-of-ways. Found throughout the area.

Asclepias viridiflora Raf. Common, in rocky upland prairies and on rocky prairie slopes. Found throughout the area.

Asclepias viridis Walt. Common, in upland prairies and on rocky prairie slopes. Encountered throughout the area.

Cynanchum laeve (Michx.) Pers. Occasional, in floodplain woods. Occurs throughout the area.

CONVOLVULACEAE

Convolvulus arvensis L. Common, in overgrazed prairies, cultivated fields, waste places, along right-of-ways and roadsides. Occurs throughout the area.

Convolvulus sepium L. Common, in moist soil of prairie canyons, margins of impoundments, prairie hay meadows, wooded fence rows, along railway right-of-ways and roadsides. Found throughout the area.

Cuscuta cephalanthi Engelm. Occasional, in moist ground on coarse herbs and shrubs. Reported for Marshall County by Gates (1940).

Cuscuta coryli Engelm. Occasional, in moist ground on coarse herbs and shrubs. Reported for Pottawatomie County by Gates (1940).

Cuscuta glomerata Choisy. Common, in moist ground on coarse herbs and shrubs. Found throughout the area.

Cuscuta gronovii Willd. Occasional, in moist ground on coarse herbs and shrubs. Reported for Marshall County by Gates (1940).

Cuscuta indecora Choisy. Occasional, in moist ground on coarse herbs and shrubs. Reported for Geary County by Gates (1940).

Cuscuta pentagona Engelm. Occasional, in moist ground on coarse herbs and shrubs. Reported for Cowley and Riley counties by Gates (1940).

Cuscuta polygonorum Engelm. Occasional, in moist ground on coarse herbs and shrubs. Known from Geary, Pottawatomie, Riley and Wabaunsee counties.

Evolvulus nuttallianus R. & S. Common, in rocky upland prairies and on rocky, prairie slopes. Found throughout the area.

Ipomoea hederacea (L.) Jacq. Common, in cultivated fields, waste places, stream valley woods and along roadsides. Found throughout the area.

Ipomoea lacunosa L. Occasional, in cultivated fields, waste places, stream valley woods and along roadsides. Known from Cowley, Morris, Pottawatomie and Riley counties.

Ipomoea leptophylla Torr. Rare, in sandy soil along streams and in low prairies. Reported for Riley County by Gates (1940).

Ipomoea pandurata (L.) G. F. W. Meyer. Occasional, in cultivated fields, waste places, rocky prairie slopes and along roadsides. Found throughout the area.

Ipomoea purpurea (L.) Roth. Common, in cultivated fields, waste places, floodplain woods and along roadsides. Occurs throughout the area.

POLEMONIACEAE

Phlox bifida Beck. Rare, in wooded canyons. Reported for Pottawatomie County by Gates (1940).

Phlox divaricata L. var. *laphamii* Wood. Common, in wooded canyons and floodplain woods. Found throughout the area.

Phlox oklahomensis Wherry. Occasional, in rocky upland prairies, on rocky prairie slopes and along rocky roadside embankments. Known from Butler and Cowley counties.

Phlox pilosa L. var. *fulgida* Wherry. Occasional, in upland prairies, prairie hay meadows and prairie canyons. Known from Marshall and Riley counties.

HYDROPHYLLACEAE

Ellisia nyctelea L. Common, in floodplain woods, low cultivated ground and low waste places. Found throughout the area.

Hydrophyllum virginianum L. Occasional, in rich woods along streams. Known from Pottawatomie County.

BORAGINACEAE

Cynoglossum officinale L. Rare, in overgrazed prairies, rocky waste places, and along roadsides. Reported for Geary and Riley counties by Gates (1940).

Echium vulgare L. Rare, in waste places and along roadsides. Reported for Pottawatomie and Riley counties by Gates (1940).

Hackelia virginiana (L.) Johnst. Common, on open wooded slopes, in floodplain woods and lowland waste places. Found commonly in the northern part of the area while only occasionally in the southern part.

Heliotropium tenellum (Nutt.) Torr. Occasional, in rocky upland prairies, on rocky prairie slopes and often growing in the crevices of outcropping limestone rocks. Known from Butler and Cowley counties.

Lappula echinata Gilib. Rare, in waste places and cultivated fields. Reported to be in the Kansas River valley in Riley County by Gates (1940).

Lappula redowskii (Hornem.) Greene var. *occidentalis* (Wats.) Rydb. Rare, in waste places, along railroad right-of-ways, and in cultivated fields. Occurs in Geary, Pottawatomie and Riley counties.

Lithospermum arvense L. Occasional, in waste places, cultivated fields, overgrazed prairies, along roadsides and railroad right-of-ways. Found in Cowley and Chase counties.

Lithospermum canescens (Michx.) Lehm. Occasional, in rocky prairies, open wooded areas on slopes and along roadsides. Known from Chase, Marshall and Riley counties.

Lithospermum incisum Lehm. Common, in rocky prairie, on rocky prairie slopes, open wooded areas on rocky slopes and along prairie roadsides. Occurs throughout the area.

Myosotis virginica (L.) BSP. Rare, in cultivated fields, open wooded areas, along roadsides and railroad right-of-ways. Reported for Lyon and Pottawatomie counties by Gates (1940).

Onosmodium molle Michx. Common, in rocky upland prairies, on rocky prairie slopes and in open wooded areas on rocky slopes. Found throughout the area.

VERBENACEAE

Lippia cuneifolia (Torr.) Steud. Rare, along the margins of impoundments and streams. Reported for Geary, Riley and Wabaunsee counties by Gates (1940).

Lippia lanceolata Michx. Occasional, along drainage areas, margins of impoundments and streams. Occurs throughout the area.

Verbena bipinnatifida Nutt. Occasional, in rocky upland prairies, along roadsides and railway right-of-ways. Reported for Cowley, Geary, Pottawatomie, Riley and Wabaunsee counties by Gates (1940).

Verbena bracteata Lag. & Rodr. Occasional along roadsides, cultivated fields and railway right-of-ways. Found throughout the area.

Verbena canadensis (L.) Britt. Common, in rocky upland prairies, on rocky prairie slopes, on rocky roadside embankments and along railroad right-of-ways. Found throughout the area.

Verbena hastata L. Occasional, along prairie drainage areas, in low prairie canyons, along margins of impoundments and streams. Occurs throughout the area.

Verbena simplex Lehm. Occasional in rocky upland prairies, on rocky prairie slopes, along roadsides and railway right-of-ways. Found in Butler, Chase, Cowley, Lyon and Wabaunsee counties.

Verbena stricta Vent. Common, in upland prairies, on prairie slopes, along roadsides and railroad right-of-ways. Occurs throughout the area.

Verbena urticifolia L. Common, in floodplain woods and on wooded slopes. Found throughout the area.

LABIATAE

Agastache nepetoides (L.) Ktze. Occasional, in wooded canyons and rich woods along drainage areas and streams. Found throughout the area.

Glechoma hederacea L. Rare, in waste places and thickets. Reported for Riley County by Gates (1940).

Hedeoma hispida Pursh. Common, in rocky upland prairies, on rocky prairie slopes, in prairie canyons, waste places, along railway right-of-ways and roadsides. Found throughout the area.

Isanthus brachiatus (L.) BSP. Rare, along streambeds, on moist limestone escarpments in prairie areas and in roadside ditches. Known from Chase, Cowley, Geary, Marshall, Pottawatomie, Riley and Wabaunsee counties.

Lamium amplexicaule L. Common, in lawns, waste places, overgrazed prairies, prairie hay meadows, along railway right-of-ways and roadsides. Occurs throughout the area.

Leonurus cardiaca L. Occasional, in cultivated fields, waste places, about farm dwellings, in overgrazed pastures and along roadsides. Found in Marshall, Pottawatomie, Riley and Wabaunsee counties.

Lycopus americanus Muhl. Common, in rich woods along streams, drainage areas and along margins of impoundments. Found throughout the area.

Lycopus asper Greene. Rare, in wet soil especially in thickets. Reported for Marshall and Riley counties by Gates (1940).

Lycopus uniflorus Michx. Rare, in moist soil. Reported for Pottawatomie County by Gates (1940).

Lycopus virginicus L. Rare, in low wet woods and open ground. Reported for Pottawatomie and Riley counties by Gates (1940).

Marrubium vulgare L. Occasional, in cultivated fields, waste ground, overgrazed prairies, and around old dwellings. Found throughout the area.

Mentha arvensis L. Occasional, in wet soil along springs, drainage areas, streams and impoundments. Found throughout the area.

Monarda citriodora Cerv. Common, in rocky upland prairies and on rocky prairie slopes. Known from Butler, Chase, Cowley and Lyon counties.

Monarda fistulosa L. var. *mollis* (L.) Benth. Common to abundant, in rocky upland prairies, along limestone escarpments on prairie slopes and sometimes in open wooded canyons. Found throughout the area.

Nepeta cataria L. Occasional, in cultivated fields, waste places, open woodlands and along roadsides. Found throughout the area.

Perilla frutescens (L.) Britt. Rare, in cultivated fields, waste places and in rich woods along streams. Reported for Riley County by Gates (1940).

Physostegia virginiana (L.) Benth. Rare, in moist places in upland prairies, along railway right-of-ways and roadsides. Reported for Pottawatomie and Riley counties by Gates (1940).

Prunella vulgaris L. Common, along drainage areas, streambanks, impoundments and in roadside ditches. Found throughout the area.

Pycnanthemum flexuosum (Walt.) BSP. Rare, in upland prairies, prairie hay meadows, prairie canyons and sometimes in open woodlands. Reported for Riley County by Gates (1940).

Pycnanthemum virginianum (L.) Durand & Jackson. Rare, in rocky woods and thickets. Reported for Pottawatomie County by Gates (1940).

Salvia azurea Lam. var. *grandiflora* Benth. Common, in rocky upland prairies, prairie hay meadows, on rocky prairie slopes, railway right-of-ways and roadsides. Occurs throughout the area.

Salvia reflexa Hornem. Common, in cultivated fields, overgrazed prairie pastures, waste places and rocky roadsides. Found throughout the area.

Scutellaria lateriflora L. Rare, along streams and impoundments. Known from Butler, Pottawatomie and Riley counties.

Scutellaria parvula Michx. var. *australis* Fasset. Occasional, in rocky upland prairies and on rocky prairie slopes. Found throughout the area.

Scutellaria parvula Michx. var. *leonardi* (Epling) Fern. Occasional, in rocky upland prairies and on rocky prairie slopes. Found throughout the area.

Stachys tenuifolia Willd. Rare, in floodplain woods and wooded canyons. Reported Pottawatomie and Riley counties by Gates (1940).

Teucrium canadense L. Common, in prairies, prairie hay meadows, wooded canyons, along railway right-of-ways and roadsides. Found throughout the area.

SOLANACEAE

Datura metel L. Rare, in waste ground. Reported for Morris and Riley counties by Gates (1940).

Datura stramonium L. Occasional to common, in farmyards, cultivated fields, waste ground and open floodplains. Occurs throughout the area.

Lycium halimifolium Mill. Rare, escapes from cultivation to waste ground and along roadsides. Reported for Marshall, Riley and Wabaunsee counties by Gates (1940).

Physalis angulata L. var. *pendula* (Rydb.) Waterfall. Occasional, in open alluvial soil in lowland areas, cultivated fields, waste ground and along roadsides. Found in Butler, Chase, Marion, Morris and Riley counties.

Physalis hederaefolia Gray var. *comata* (Rydb.) Waterfall. Rare, in prairie areas. Reported for Geary and Riley counties by Gates (1940).

Physalis heterophylla Nees. Occasional, in overgrazed prairies, open areas in wooded canyons, waste ground and along roadsides. Found throughout the area.

Physalis ixocarpa Brot. Rare, along railroad right-of-ways. Reported for Pottawatomie and Riley counties by Gates (1940).

Physalis longifolia Nutt. var. *subglabrata* (Mackenz. & Bush) Cronq. Occasional, in overgrazed prairies, open areas in wooded canyons, waste ground and along roadsides. Encountered throughout the area.

Physalis missouriensis Mackenz. & Bush. Rare, in rich stream valley woods. Reported for Geary, Marshall, Pottawatomie and Riley counties by Gates (1940).

Physalis pubescens L. Rare, in rocky wooded canyons, cultivated fields, waste ground and along roadsides. Known from Chase, Geary and Riley counties.

Physalis pumila Nutt. Occasional, in rocky upland prairies, along roadsides and railway right-of-ways. Found throughout the area.

Physalis virginiana Mill. Occasional, in rocky wooded canyons, waste ground and along roadsides. Occurs throughout the area.

Solanum carolinense L. Occasional, in waste ground, cultivated fields, overgrazed prairies and along roadsides. Occurs throughout the area.

Solanum elaeagnifolium Cav. Occasional, in waste ground, cultivated fields, overgrazed prairies and along roadsides. Found throughout the area.

Solanum rostratum Dunal. Common, in farmyards, severely overgrazed prairies, waste ground, cultivated fields and along the roadsides. Occurs throughout the area.

Solanum torreyi Gray. Rare, in rocky or sandy open ground. Reported for Cowley County by Gates (1940).

Solanum triflorum Nutt. Rare, in waste ground, cultivated fields and along roadsides. Reported for Riley County by Gates (1940).

SCHROPHULARIACEAE

Bacopa rotundifolia (Michx.) Wettst. Occasional, in alluvial soil along the margins of impoundments and streams. Known from Geary, Morris, Pottawatomie and Riley counties.

Castilleja sessiliflora Pursh. Rare, in rocky upland prairies and on rocky prairie slopes. Known from Cowley, Pottawatomie and Riley counties.

Conobea multifida Michx. Occasional, in alluvial soil along impoundments, streams, roadside ditches and in open areas of lowland woods. Occurs throughout the area.

Dasistoma macrophylla (Nutt.) Raf. Rare, in wooded canyons and rich stream valley woods. Reported for Pottawatomie, Riley and Wabaunsee counties by Gates (1940).

Gerardia aspera Dougl. Occasional, in moist upland prairies. Known from Butler, Chase, Geary, Morris, Pottawatomie and Riley counties.

Gerardia densiflora Benth. Rare, in rocky upland prairie and on rocky prairie slopes. Known from Chase and Lyon counties.

Gerardia gattingeri Small. Rare, in alluvial soil in roadside ditches along the margins of impoundments and streams. Found in Wabaunsee County.

Gerardia tenuiflora Vahl. Occasional, in alluvial soil in roadside ditches, drainage areas, along margins of impoundments and streams. Occurs in Morris, Pottawatomie, Riley and Wabaunsee counties.

Linaria vulgaris Hill. Occasional, in cultivated fields, overgrazed pastures, waste ground and along roadsides. Known from Pottawatomie and Riley counties.

Lindernia anagallidea (Michx.) Pennell. Occasional, in alluvial soil along drainage areas, margins of impoundments and streams. Found in Butler and Cowley counties.

Lindernia dubia (L.) Pennell. Occasional, in alluvial soil along drainage areas, margins of impoundments and streams. Known from Cowley, Morris, Pottawatomie and Riley counties.

Mimulus alatus Ait. Rare, in alluvial soil along drainage areas, margins of impoundments and streams. Collected from Butler and Pottawatomie counties.

Mimulus glabratus HBK. Occasional, in alluvial soil along margins of impoundments and streams. Found in Butler, Geary, Pottawatomie, Riley and Wabaunsee counties.

Mimulus ringens L. Occasional, in alluvial soil along drainage areas, margins of impoundments and streams. Encountered in Pottawatomie, Riley and Wabaunsee counties.

Penstemon cobaea Nutt. Common, in rocky upland prairies, on rocky prairie slopes and in open areas of wooded canyons. Found throughout the area.

Penstemon digitalis Nutt. Rare, in upland prairies and on rocky prairie slopes. Known from Butler County.

Penstemon grandiflorus Nutt. Occasional, in rocky upland prairies, on rocky prairie slopes and in open areas of wooded canyons. Occurs throughout the area.

Penstemon tubaeflorus Nutt. Occasional, in upland prairies, prairie hay meadows and in prairie canyons. Found in Cowley, Lyon, Morris and Riley counties.

Scrophularia lanceolata Pursh. Rare, in rich floodplain woods. Reported for Riley County by Gates (1940).

Scrophularia marilandica L. Common, in floodplain woods. Occurs throughout the area.

Verbascum blattaria L. Occasional, in cultivated fields, waste ground, severely overgrazed prairies and along roadsides. Encountered throughout the area.

Verbascum thapsus L. Common to abundant, along cultivated fields, in waste ground, severely overgrazed prairies and along roadsides. Found throughout the area.

Veronica anagallis-aquatica L. Rare, in alluvial soil along the margins of impoundments and streams. Known from Cowley County.

Veronica arvensis L. Common, in cultivated fields, waste ground, severely overgrazed prairies and along roadsides. Occurs throughout the area.

Veronica catenata Pennell. Rare, in water and wet places. Reported for Morris and Riley counties by Gates (1940).

Veronica peregrina L. Common, in cultivated fields, waste ground, severely overgrazed prairies and along the roadsides. Encountered throughout the area.

Veronica polita Fries. Rare, in cultivated fields, waste ground, severely overgrazed prairies and along the roadsides. Reported for Geary County by Gates (1940).

Veronica triphylos L. Rare, in waste ground. Reported for Geary County by Gates (1940).

BIGNONIACEAE

Campsis radicans (L.) Seem. Occasional, in floodplain woods, and around abandoned farmyards. Often cultivated. Found throughout the area.

Justicia americana (L.) Vahl. Common, grows at the margins of streams or impoundments, either in shallow water or mud. Found throughout the area.

Ruellia humilis Nutt. Common, in upland prairies, prairie hay meadows and prairie canyons. Found throughout the area.

Ruellia strepens L. Common, in dense floodplain woods. Found throughout the area.

PHRYMACEAE

Phryma leptostachya L. Occasional, in wooded canyons and stream valley woods. Throughout the area.

PLANTAGINACEAE

Plantago aristata Michx. Occasional, in overgrazed prairies, open wooded canyons, along roadsides and railroad right-of-ways. Found in Butler, Lyon, Morris, Riley and Wabaunsee counties.

Plantago lanceolata L. Occasional, in lawns, cultivated fields, waste ground and along roadsides. Known from Lyon, Riley and Wabaunsee counties.

Plantago patagonica Jacq. Common, in overgrazed prairies, waste places and along the roadsides. Throughout the area.

Plantago rhodosperma Dcne. Occasional, in overgrazed prairies and waste ground. Occurs throughout the area.

Plantago rugellii Dcne. Common, in lawns, cultivated fields, overgrazed prairies, waste places and along the roadsides. Throughout the area.

Plantago virginica L. Occasional, in overgrazed prairies and waste ground. Encountered throughout the area.

RUBIACEAE

Cephalanthus occidentalis L. Common, in floodplain woods, along the margins of impoundments and streams. Occurs throughout the area.

Diodia teres Walt. Rare, in rocky soil of prairie drainage areas, alluvial soil along impoundments and streams. Known from Butler and Wabaunsee counties.

Galium aparine L. Common, in wooded canyons and in stream valley woods. Found throughout the area.

Galium circaezans Michx. Common, in rocky wooded canyons and in stream valley woods. Occurs throughout the area.

Galium concinnum T. & G. Rare, in wooded canyons and moist stream valley woods. Known from Wabaunsee County.

Galium triflorum Michx. Rare, in wooded canyons. Known from Wabaunsee County.

Galium virgatum Nutt. Occasional, in rocky upland prairie areas, on rocky prairie slopes and on rocky roadside embankments. Known from Cowley County.

Hedyotis nigricans (Lam.) Fosberg. Common, in rocky upland prairies, on rocky prairie slopes, in prairie hay meadows and along prairie railway right-of-ways. Occurs throughout the area.

CAPRIFOLIACEAE

Sambucus canadensis L. Common, in moist floodplain woods, wooded canyons, along streambanks, fence rows, roadsides and railway right-of-ways. Occurs throughout the area.

Symphoricarpos orbiculatus Moench. Common, in floodplain woods, wooded canyons, wooded slopes and overgrazed prairies. Encountered throughout the area.

Triosteum perfoliatum L. Occasional, in wooded canyons and on wooded slopes. Known from Cowley, Morris and Wabaunsee counties.

Viburnum rufidulum Raf. Occasional, in stream valley woods and in wooded canyons. Known from Cowley County.

CUCURBITACEAE

Cucurbita foetidissma HBK. Occasional, in overgrazed prairies, along railway right-of-ways and roadsides. Found throughout the area.

Echinocystis lobata (Michx.) T. & G. Occasional, in floodplain woods along drainage areas and streams, along roadsides and in low waste places. Occurs throughout the area.

Melothria pendula L. Rare, in floodplain wooded areas. Known from Cowley County.

Sicyos angulatus L. Common, in stream valley woods, along drainage areas, in wooded canyons, along roadsides and railroad right-of-ways. Encountered throughout the area.

CAMPANULACEAE

Campanula americana L. Common, in floodplain woods, moist wooded canyons and along the margins of wooded areas. Occurs throughout the area.

Triodanis leptocarpa (Nutt.) Nieuwl. Common, in moist upland prairies, along prairie drainage areas and in prairie canyons. Found throughout the area.

Triodanis perfoliata (L.) Nieuwl. Common, in moist upland prairies, along prairie drainage areas, in prairie canyons, open alluvial soil along streams and along roadsides. Encountered throughout the area.

LOBELIACEAE

Lobelia cardinalis L. Occasional, along wet streambanks, seepage areas and in wet roadside ditches. Known from Butler, Chase, Cowley and Pottawatomie counties.

Lobelia siphilitica L. Occasional, along wet streambanks, margins of impoundments, seepage areas, drainage areas and roadside ditches. Found in Marshall, Pottawatomie and Wabaunsee counties.

Lobelia spicata Lam. var. *hirtella* Gray. Common, in moist upland prairies, along drainage areas and in prairie canyons. Occurs throughout the area.

Lobelia spicata Lam. var. *leptostachys* (A. DC.) Mackenz. & Bush. Common, in moist upland prairies, along drainage areas and in prairie canyons. Found throughout the area.

COMPOSITAE

Achillea millefolium L. Common, in upland prairies, abandoned fields, waste places and along roadsides. Found throughout the area.

Ambrosia artemisiifolia L. Common to abundant, in cultivated fields, abandoned fields, severely overgrazed pastures, waste places, along roadsides and railway right-of-ways. Occurs throughout the area.

Ambrosia bidentata Michx. Occasional, in roadside ditches, overgrazed prairies, waste places and along the margins of impoundments. Known from Cowley County.

Ambrosia psilostachya DC. Occasional, in roadside ditches and overgrazed prairies. Found throughout the area.

Ambrosia trifida L. Common to abundant, in waste places, low wooded areas, fallow fields, cultivated fields, along streams, roadsides and railroad right-of-ways. Occurs throughout the area.

Antennaria neglecta Greene. Common, in rocky upland prairies, prairie hay meadows, on rocky prairie slopes and in dry, open wooded areas. Found throughout the area.

Antennaria plantaginifolia (L.) Richards. Occasional, in rocky wooded canyons. Found in Pottawatomie, Riley and Wabaunsee counties.

Anthemis cotula L. Occasional, introduced in overgrazed prairies, farmyards, cultivated fields, waste ground, roadsides and railroad right-of-ways. Scattered throughout the area.

Arctium minus Schk. Occasional, in waste places, farmyards, disturbed wooded areas, and along railroad right-of-ways. Known from the northern part of the area.

Artemisia biennis Willd. Rare, in alluvial soil of floodplain woods. Reported for Marshall, Pottawatomie and Riley counties by Gates (1940).

Artemisia ludoviciana Nutt. Common, in rocky upland prairies, on rocky prairie slopes, in open canyon woods, along roadsides and railway right-of-ways. Found throughout the area.

Aster azureus Lindl. Occasional, in rocky prairies, along prairie roadsides and in open wooded canyons. Occurs in Pottawatomie, Riley and Wabaunsee counties.

Aster drummondii Lindl. Common, in floodplain woods, wooded canyons and along wooded fence rows. Occurs throughout the area.

Aster ericoides L. Common to abundant, in rocky upland prairies, on rocky prairie slopes, in prairie canyons, along roadsides, railway right-of-ways and sometimes in rocky, open wooded areas on the slopes. Found throughout the area.

Aster laevis L. Occasional, in rocky upland prairies, on dry wooded, rocky slopes and along roadsides. Occurs throughout the area.

Aster novae-angliae L. Rare, in low, alluvial ground along streams, and in low moist prairies. Reported for Riley County by Gates (1940).

Aster oblongifolius Nutt. Common, in rocky upland prairies, on rocky prairie slopes, along roadsides and railroad right-of-ways. Encountered throughout the area.

Aster pilosus Willd. Occasional, in cultivated fields, abandoned fields, prairie hay meadows, disturbed rocky prairies and along roadsides. Found in Pottawatomie and Marion counties.

Aster praealtus Poir. Common, in moist canyon prairies, along prairie drainage areas, seepage areas and in moist roadside ditches. Found in the northern part in Cowley County.

Aster sericeus Vent. Common, in rocky upland prairies and on rocky prairie slopes. Occurs throughout the area.

Aster simplex Willd. Common, in moist prairie areas, along drainage areas, seepage areas, fence rows, margins of floodplain woods and moist roadside ditches. Encountered throughout the area.

Aster vimineus Lam. Rare, in moist prairie canyons, and alluvial soil along drainage areas, streams and man-made impoundments. Known from Chase County.

Bidens bipinnata L. Occasional, in open wooded areas, moist areas in prairies, along roadsides and railway right-of-ways. Known from Cowley and Pottawatomie counties.

Bidens cernua L. Occasional, wet places along streams, drainage areas and impoundments. Found in Riley and Marshall counties.

Bidens comosa (Gray) Wieg. Occasional, wet places along drainage areas, streams and impoundments. Collected from Pottawatomie, Riley and Wabaunsee counties.

Bidens frondosa L. Common, in floodplain woods, wet lowland prairies, along drainage areas, streams, impoundments and roadside ditches. Found throughout the area.

Bidens polylepis Blake. Common, in alluvial soil along streams, drainage areas, impoundments, in cultivated fields, waste ground and roadside ditches. Found throughout the area.

Bidens vulgata Greene. Common, in alluvial soil along drainage areas, streams, impoundments, waste places and roadside ditches. Found in the northern part.

Boltonia asteroides (L.) L'Her var. *latisquama* (Gray) Cronq. Occasional, in wet prairie canyons, along drainage areas, streams and roadside ditches. Known from throughout the area.

Cacalia atriplicifolia L. Occasional, in floodplain woods, along streambanks, drainage areas, in open canyon woods and in wet roadside ditches. Found in the northern part and in Cowley County.

Cacalia tuberosa Nutt. Common, in upland prairies, prairie hay meadows, and in prairie canyons. Occurs throughout the area.

Carduus nutans L. Common to abundant, in severely overgrazed prairies, on rocky prairie slopes, in cultivated fields, abandoned fields and other waste places. A common noxious weed found in the northern part of the area, that is spreading southward.

Centaurea americana Nutt. Rare, in rocky prairies, open wooded areas, along roadsides and railway right-of-ways. Reported for Butler County by Gates (1940).

Centaurea cyanus L. Rare, escapes from cultivation into roadsides, overgrazed prairies, cultivated fields and other waste places. Reported for Riley County by Gates (1940).

Centaurea repens L. Rare, in waste places and cultivated ground. Reported for Cowley and Riley counties by Gates (1940).

Chrysanthemum balsamita L. Rare, escapes from cultivation into waste places. Reported for Riley County by Gates (1940).

Chrysanthemum leucanthemum L. Common, in cultivated fields, prairie hay meadows, grazed prairies, open wooded areas, along railroad right-of-ways and roadsides. Found throughout the area.

Chrysopsis villosa (Pursh.) Nutt. Rare, in rocky prairies and prairie roadsides. Found in Butler County.

Cichorium intybus L. Occasional, in cultivated fields, along roadsides, railway right-of-ways and other waste places. Known from Morris, Pottawatomie and Riley counties.

Cirsium altissimum (L.) Spreng. Common, in wooded canyons, stream valley woods, wet places along roadsides and railroad right-of-ways. Occurs throughout the area.

Cirsium undulatum (Nutt.) Spreng. Common, in upland prairies, prairie canyons, along roadsides and railroad right-of-ways. Found throughout the area.

Cirsium vulgare (Savi) Tenore. Rare, in cultivated fields, grazed prairies, waste places and along roadsides. Reported for Wabaunsee County by Gates (1940).

Conyza canadensis (L.) Cronq. Common, in cultivated fields, abandoned fields, overgrazed prairies, waste places, along roadsides and railroad right-of-ways. Found throughout the area.

Conyza ramosissima Cronq. Occasional, in cultivated fields, rocky overgrazed prairies, waste places, along railroad right-of-ways and roadsides. Occurs throughout the area.

Coreopsis grandiflora Hogg. Occasional, in upland prairies, prairie canyons and in open wooded areas. Known from Cowley County.

Coreopsis tinctoria Nutt. Occasional, in sandy soil along streams, cultivated fields, along roadsides and railroad right-of-ways. Found throughout the area.

Dyssodia papposa (Vent.) Rydb. Common, in cultivated fields, overgrazed prairies, along railroad right-of-ways and roadsides. Found throughout the area.

Echinacea angustifolia DC. Common, in rocky upland prairies, on rocky prairie slopes and along prairie roadsides. Occurs throughout the area.

Echinacea atrorubens Nutt. Occasional, in upland prairies, prairie hay meadows along prairie roadsides and railroad right-of-ways. Found in Butler, Cowley, Lyon and Wabaunsee counties.

Echinacea pallida Nutt. Common, in rocky upland prairies, on rocky prairie slopes along prairie roadsides and railroad right-of-ways. Found in the southern part.

Eclipta alba (L.) Hassk. Occasional, along the margin of streams, impoundments and in wet roadside ditches. Known from Butler, Cowley and Lyon counties.

Erechtites hieracifola (L.) Raf. Rare, along streambanks, in open woods and waste places. Reported for Pottawatomie and Riley counties by Gates (1940).

Erigeron annuus (L.) Pers. Common, in upland prairies, prairie hay meadows, prairie canyons, waste places, along railroad right-of-ways and roadsides. Found throughout the area.

Erigeron philadelphicus L. Common, in cultivated fields, stream valley woods, moist prairie canyons, prairie hay meadows, along railway right-of-ways and roadsides. Occurs throughout the area.

Erigeron strigosus Muhl. Common, in rocky upland prairies, on rocky prairie slopes, along railroad right-of-ways and roadsides. Found throughout the area.

Eupatorium altissimum L. Common, in upland prairies, along prairie roadsides, in wooded canyons and stream valley woods. Found throughout the area.

Eupatorium maculatum L. Rare, creek valley woods. Reported for Pottawatomie County by Gates (1940).

Eupatorium perfoliatum L. Rare, in rich woods along streams and in wooded canyons. Reported for Pottawatomie and Riley counties by Gates (1940).

Eupatorium rugosum Houtt. Common, in rich woods along streams and wooded canyons. Found throughout the area.

Evax prolifera Nutt. Rare, in rocky upland prairies and on rocky prairie slopes. Known from Cowley County.

Franseria tomentosa A. Gray. Rare, in prairie canyons and moist places in upland prairies. Reported for Marion County by Gates (1940).

Gaillardia pulchella Foug. Rare, in sandy soil along the Kansas and Arkansas Rivers and along railroad right-of-ways in Cowley and Riley counties.

Galinsoga ciliata (Raf.) Blake. Rare, a weed of gardens, yards and waste places. Reported for Pottawatomie County by Gates (1940).

Galinsoga parviflora Cav. Rare, in waste places. Reported for Riley County by Gates (1940).

Gnaphalium obtusifolium L. Occasional, in abandoned fields, overgrazed prairies, open woodlands, along railway right-of-ways and roadsides. Found throughout the area.

Grindelia lanceolata Nutt. Rare, in overgrazed, rocky prairies, along railroad right-of-ways and roadsides. Known from Cowley County.

Grindelia squarrosa (Pursh.) Dunal. Common, in waste places, overgrazed prairies, open stream valley woods, along railroad right-of-ways and roadsides. Known from all counties except, Cowley and Butler counties.

Gutierrezia dracunculoides (DC.) Blake. Common, in overgrazed prairies, cultivated fields, waste places, along railroad right-of-ways and roadsides. Occurs throughout the area.

Haplopappus ciliatus (Nutt.) D.C. Occasional, in upland prairies, prairie canyons, open floodplains and low waste places. Found in Butler, Chase, Cowley, Lyon and Riley counties.

Helenium amarum (Raf.) Rock. Rare, in cultivated fields, waste grounds, along railroad right-of-ways and roadsides. Known from Butler, Pottawatomie and Wabaunsee counties.

Helianthus annuus L. Common, in cultivated fields, abandoned fields, waste places, overgrazed lowland prairies, along railway right-of-ways and roadsides. Encountered throughout the area.

Helianthus grosseserratus Martens. Common, in upland prairies, prairie canyons, along fence rows, margins of impoundments, railroad right-of-ways and roadsides. Occurs throughout the area.

Helianthus hirsutus Raf. Common, in wooded canyons, stream valley woods, and along wooded roadsides. Known from throughout the area.

Helianthus laetiflorus Pers. var. *rigidus* (Cass.) Fern. Common, in rocky upland prairies, on rocky prairie slopes, along railroad right-of-ways and roadsides. Occurs throughout the area.

Helianthus maximiliani Schrader. Common, in rocky upland prairies, on rocky prairie slopes, in waste places, along railway right-of-ways and roadsides. Occurs throughout the area.

Helianthus mollis Lam. Rare, in prairie areas, thickets and barren ground. Reported for Riley County by Gates (1940).

Helianthus petiolaris Nutt. Occasional, in overgrazed prairies, open areas along streams, waste places, along railway right-of-ways and roadsides. Known from Chase, Cowley, Riley and Wabaunsee counties.

Helianthus salicifolius A. Dietr. Common, in rocky upland prairies, along the limestone escarpments on the prairie slopes, along railway right-of-ways and roadsides. Found throughout the area.

Helianthus tuberosus L. Common, in wooded areas along streams and in wooded canyons. Found throughout the area.

Heliopsis helianthoides (L.) Sweet. Common, in stream valley woods, wooded canyons, along wooded fence rows, railway right-of-ways and roadsides. Encountered throughout the area.

Heterotheca latifolia Buckl. Rare, in sandy alluvial soil along the Arkansas River floodplain. Known from Cowley County.

Hieracium longipilum Torr. Occasional, in moist upland prairies and in prairie lowlands. Occurs throughout the area.

Hymenopappus scabiosaeus L'Her. Common, in rocky upland prairies, along limestone escarpments and in roadside ditches. Encountered throughout the area.

Iva annua L. Occasional to common, in alluvial soil along streams, impoundments, in prairie canyons, roadside ditches and railroad right-of-ways. Found throughout the area.

Iva xanthifolia Nutt. Rare, in waste places and along streams. Reported for Riley County by Gates (1940).

Krigia oppositifolia Raf. Rare, in prairies, thickets and open sandy ground. Reported for Morris, Riley and Wabaunsee counties by Gates (1940).

Kuhnia eupatorioides L. Common, in overgrazed upland prairies, on rocky prairie slopes, in open wooded canyons, and along rocky roadside embankments. Occurs throughout the area.

Lactuca canadensis L. Common, in wooded canyons, along impoundments, streams, lowland fields and roadsides. Encountered throughout the area.

Lactuca floridana (L.) Gaertn. Occasional, in rich woods along streams, wet lowland areas and along roadsides. Found throughout the area.

Lactuca ludoviciana (Nutt.) DC. Common, in rich wooded areas along drainage areas and streams. Found throughout the area.

Lactuca scariola L. Common, in cultivated fields, abandoned fields, waste places, along roadside ditches and railway right-of-ways. Occurs throughout the area.

Liatris aspera Michx. Common, in upland prairies, prairie meadows, sometimes in prairie openings in wooded areas and along railway right-of-ways. Encountered throughout the area.

Liatris mucronata DC. Common, in shallow soil above limestone outcrops in prairie areas. Known from throughout the area.

Liatris punctata Hook. Occasional, in upland prairies and along prairie roadsides. Found throughout the area.

Liatris pycnostachya Michx. Occasional, in moist places in upland prairies, low prairie hay meadows, along moist railway right-of-ways and roadsides. Known from throughout the area.

Liatris squarrosa (L.) Michx. var. *glabrata* (Rydb.) Gaiser. Rare, in upland prairies and open wooded canyons. Reported for Pottawatomie and Riley counties by Gates (1940).

Liatris squarrosa (L.) Michx. var. *hirsuta* (Rydb.) Gaiser. Rare, in upland prairies and open wooded canyons. Collected in Marshall County and reported for Marshall, Pottawatomie and Riley counties by Gates (1940).

Lygodesmia juncea (Pursh) D. Don. Rare, in sandy prairie areas. Reported for Geary and Riley counties by Gates (1940).

Microseris cuspidata (Pursh) Schulta-Bip. Occasional, in rocky upland prairies and along the roadsides. Found in Cowley, Geary, Lyon, Morris, Pottawatomie, Riley and Wabaunsee counties.

Parthenium hispidum Raf. Common, in rocky upland prairies, on rocky prairie slopes and along roadsides. Known from Butler and Cowley counties.

Prenanthes aspera Michx. Common, in open wooded canyons and rocky prairie areas. Found throughout the area.

Pyrrhopappus carolinianus (Walt.) DC. Rare, in cultivated fields, open floodplain woods, moist railway right-of-ways and roadsides. Known from Pottawatomie and Butler counties.

Pyrrhopappus scaposus DC. Common, in upland prairies, prairie canyons, and along prairie railway right-of-ways. Found in Butler, Cowley and Riley counties.

Ratibida columnifera (Nutt.) Woot. & Standl. Common, in upland prairies, on rocky prairie slopes, in prairie canyons, along railroad right-of-ways and roadsides. Occurs throughout the area.

Ratibida pinnata (Vent.) Barnh. Rare, in wooded areas along streams, wooded canyons and along the margins of wooded areas. Known from Lyon, Marshall and Wabaunsee counties.

Rudbeckia amplexicaulis Vahl. Rare, in moist prairies, sandy soil along Arkansas River floodplain, and along roadsides. Known from Cowley County.

Rudbeckia hirta L. Occasional to common, in open wooded canyons, prairie canyons, prairie hay meadows and along railway right-of-ways. Occurs throughout the area.

Rudbeckia laciniata L. Rare, in low open woods and wooded areas along streams. Reported for Marshall, Pottawatomie and Riley counties by Gates (1940).

Rudbeckia triloba L. Rare, in wooded plains along streams and in canyon wooded areas. Known from Lyon County.

Senecio plattensis Nutt. Common, in upland prairies, prairie hay meadows, prairie canyons and along railway right-of-ways. Encountered throughout the area.

Silphium integrifolium Michx. Common, in open places of wooded canyons, rocky prairie canyons and along railway right-of-ways. Encountered throughout the area.

Silphium laciniatum L. Common, in well-managed upland prairies, prairie hay meadows and prairie canyons. Occurs throughout the area.

Silphium perfoliatum L. Occasional, in wooded areas along streams, along impoundments and moist railroad right-of-ways. Known from Marshall, Pottawatomie and Riley counties.

Silphium speciosum Nutt. Occasional to common, in upland prairies, on rocky prairie slopes, in prairie canyons, along railway right-of-ways and roadside ditches. Found throughout the area.

Solidago altissima L. Common, in waste places, cultivated fields, abandoned fields, overgrazed prairies, open wooded canyons, along railroad right-of-ways and roadsides. Found throughout the area.

Solidago canadensis L. var. *gilvocanescens* Rydb. Occasional, in cultivated fields, abandoned fields and open stream valley woods. Occurs throughout the area.

Solidago gigantea Ait. var. *serotina* (Kuntze.) Cronq. Occasional, in floodplain woods, margins of impoundments and in wet places of prairie canyons. Encountered throughout the area.

Solidago graminifolia (L.) Salisb. Common, in overgrazed, upland prairies, cultivated fields and along railroad right-of-ways. Found throughout the area.

Solidago gymnospermoides (Greene) Fern. Occasional, in overgrazed prairies and along railway right-of-ways. Known from Chase, Pottawatomie, Riley and Wabaunsee counties.

Solidago missouriensis Nutt. var. *fasciculata* Holzinger. Common, in rocky upland prairies, on rocky prairie slopes and on rocky roadside embankments. Occurs throughout the area.

Solidago nemoralis Ait. Occasional, in open canyon woods, on rocky prairie slopes and along railroad right-of-ways and roadsides. Known from the northern part of the area.

Solidago petiolaris Ait. Occasional to common, in rocky upland prairies, on prairie slopes, along railroad right-of-ways and roadsides. Occurs commonly in the northern part of the area, while only occasionally in the southern part.

Solidago rigida L. var. *rigida*. Common, in overgrazed prairies, cultivated fields, abandoned fields, along railroad right-of-ways and roadsides. Found throughout the area.

Solidago rigida L. var. *humilis* Porter. Occasional, in overgrazed prairies, cultivated fields, abandoned fields, along railroad right-of-ways and roadsides. Known from Lyon and Riley counties.

Solidago speciosa Nutt. var. *rigidiusula* T. & G. Occasional, in rocky upland prairies, on rocky prairie slopes and along roadsides. Found throughout the area.

Solidago ulmifolia Muhl. Common, in wooded canyons and in wooded areas along streams. Known from Cowley County.

Sonchus asper (L.) Hill. Occasional, in cultivated fields, abandoned fields, waste places, farmyards, along railway right-of-ways and roadside ditches. Occurs throughout the area.

Sonchus oleraceus L. Rare, in overgrazed prairies, cultivated fields, waste places, along railway right-of-ways and roadsides. Known from Chase County.

Tanacetum vulgare L. Rare, escapes from cultivation into waste places, farmyards, prairie hay meadows, cultivated fields and along roadsides. Reported for Marshall, Morris and Pottawatomie counties.

Taraxacum erythrospermum Andrz. Common, in lawns, gardens, cultivated fields, overgrazed prairies, along railroad right-of-ways and roadsides. Occurs throughout the area.

Taraxcum officinale Wiggers. Common to abundant, in lawns, gardens, cultivated fields, overgrazed prairies, railway right-of-ways and roadside ditches. Encountered throughout the area.

Thelesperma filifolium (Hook.) A. Gray. var. *intermedium* (Rydb.) Melchert. Occasional, in rocky upland prairies and on rocky prairie slopes. Known from Butler, Chase, Cowley and Marion counties.

Thelesperma megapotamicum (Spreng.) Kuntze. Occasional to common, in rocky upland prairies and on rocky prairie slopes. Found throughout the area.

Tragopogon dubius Scop. Common, in waste places, cultivated fields, along railroad right-of-ways and roadsides. Found throughout the area.

Tragopogon porrifolius L. Occasional, in cultivated fields, abandoned fields, waste places and along roadsides. Known from Cowley, Riley and Wabaunsee counties.

Verbesina alternifolia (L.) Britt. Common, in wooded areas along streams and drainage areas. Found throughout the area.

Verbesina encelioides (Cav.) Benth. & Hook. Rare, on rocky prairie slopes and in prairie canyons. Collected once from Butler County by Dr. R. L. McGregor and reported for Riley County by Gates (1940).

Verbesina virginica L. Rare, in wooded canyons and in floodplain woods. Known from Cowley County.

Vernonia baldwini Torr. var. *interior* (Small) Schubert. Common, in upland prairies, prairie hay meadows, rocky prairie slopes, waste places, along railway right-of-ways and roadsides. Found throughout the area.

Vernonia fasciculata Michx. Occasional, in upland prairies, prairie hay meadows, prairie canyons, along railway right-of-ways and roadsides. Known from Chase, Marshall, Pottawatomie, Riley and Wabaunsee counties.

Xanthium chinense Mill. Occasional in cultivated fields, waste places, open floodplains and roadside ditches. Known from Geary, Marshall, Pottawatomie and Riley counties.

Xanthium italicum Moretti. Occasional, in cultivated fields, waste places and along roadsides. Reported for Riley County by Gates (1940).

Xanthium pennsylvanicum Wallr. Occasional, in cultivated fields, waste places and along roadsides. Known from Geary, Marshall, Morris, Pottawatomie, Riley and Wabaunsee counties.

Xanthium speciosum Kearney. Occasional in cultivated fields, waste places and along roadsides. Known from Chase and Morris counties.

STATISTICAL SUMMARY

A. Tabular list of Kansas Flint Hill plant families:

	Families	*Genera*	*Species* *Native*	*Species* *Introduced*
Pteridophytes:	Equisetaceae	1	3	..
	Ophioglossaceae	2	2	..
	Polypodiaceae	6	8	..
	Marsileaceae	1	1	..
	Totals	10	14	..
Conifers:	Cupressaceae	1	1	..
	Totals	1	1	..
Monocots:	Typhaceae	1	1	..
	Sparganiaceae	1	1	..
	Najadaceae	1	3	..
	Alistmataceae	3	6	..
	Gramineae	55	88	35
	Cyperaceae	8	55	..
	Araceae	2	2	1
	Lemnaceae	3	4	..
	Commelinaceae	2	5	..
	Pontederiaceae	1	3	..
	Juncaceae	2	6	..
	Liliaceae	11	15	1
	Iridaceae	3	2	1
	Orchidaceae	3	4	..
	Totals	96	195	38
Dicots	Salicaceae	2	8	1
	Juglandaceae	2	5	..
	Corylaceae	2	2	..
	Fagaceae	1	9	..
	Ulmaceae	2	5	1
	Moraceae	4	3	2
	Urticaceae	5	5	..
	Santalaceae	1	2	..
	Polygonaceae	3	16	7
	Chenopodiaceae	6	8	4
	Amaranthaceae	3	5	3
	Nyctaginaceae	1	3	..
	Phytolaccaceae	1	1	..
	Aizoaceae	1	..	1
	Portulacaceae	2	2	1
	Caryophyllaceae	8	4	9
	Ceratophyllaceae	1	1	1
	Nymphaceae	2	2	..
	Annonaceae	1	1	..
	Ranunculaceae	8	17	3
	Berberidaceae	1	1	..
	Menispermaceae	2	2	..
	Papaveraceae	2	..	2
	Fumariaceae	2	2	..
	Cruciferae	22	17	20
	Capparidaceae	2	2	..
	Crassulaceae	1	1	..
	Saxifragaceae	1	2	..
	Platanaceae	1	1	..
	Rosaceae	9	29	2
	Leguminosae	31	54	15
	Oxalidaceae	1	3	..

		Species	
Families	*Genera*	*Native*	*Introduced*
Geraniaceae	2	1	1
Linaceae	1	1	1
Zygophyllaceae	1	..	1
Rutaceae	2	2	..
Simarubaceae	1	..	1
Polygalaceae	1	2	..
Euphorbiaceae	5	26	2
Callitrichaceae	1	1	..
Anacardiaceae	1	4	..
Celastraceae	2	2	..
Staphyleaceae	1	1	..
Aceraceae	1	2	..
Hippocastanaceae	1	1	..
Sapindaceae	1	1	..
Balsaminaceae	1	2	..
Rhamnaceae	2	3	..
Vitaceae	3	7	..
Tiliaceae	1	1	..
Malvaceae	6	4	6
Hypericaceae	1	3	1
Elatinaceae	1	1	..
Cistaceae	2	2	..
Violaceae	2	6	1
Loasaceae	1	1	..
Cactaceae	2	3	..
Elaeagnaceae	1	1	..
Lythraceae	2	3	..
Onagraceae	7	15	..
Haloragidaceae	1	2	..
Umbelliferae	15	17	3
Cornaceae	1	3	..
Primulaceae	3	2	1
Sapotaceae	1	1	..
Ebenaceae	1	1	..
Oleaceae	1	2	..
Gentianaceae	1	1	..
Apocynaceae	1	2	..
Aslepidaceae	2	13	..
Convolvulaceae	4	12	3
Polemoniaceae	1	4	..
Hydrophyllaceae	2	2	..
Boraginaceae	8	7	4
Verbenaceae	2	9	..
Labiatae	19	20	7
Solanaceae	4	14	3
Schrophulariaceae	12	22	6
Bignoniaceae	2	1	1
Orobanchaceae	1	2	..
Lentibulariaceae	1	1	..
Martyniaceae	1	1	..
Acanthaceae	3	4	..
Phrymaceae	1	1	..
Plantaginaceae	1	5	1
Rubiaceae	4	8	..
Caprifoliaceae	4	4	..
Cucurbitaceae	4	4	..
Campanulaceae	2	3	..
Lobeliaceae	1	3	..
Compositae	61	124	20
Totals	349	604	135

B. Components of the Flora of the Kansas Flint Hills:

Major Groups of Tracheophyta	Species	Genera	Families
Pteridophytes	14	10	4
Conifers	1	1	1
Monocots	233	96	14
Dicots	739	349	91
Totals	987	456	110

C. Largest families with total number of species in each:

Compositae	144
Gramineae	123
Leguminosae	69
Cyperaceae	55
Cruciferae	37
Rosaceae	31
Euphorbiaceae	28
Schrophulariaceae	28
Labiatae	27
Polygonaceae	23
Umbelliferae	20
Ranunculaceae	20
Solanaceae	17
Liliaceae	16
Onagraceae	15
Convolvulaceae	15
Asclepidaceae	13
Caryophyllaceae	13
Chenopodiaceae	12
Boraginaceae	11

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVIII Pages 585-687 October 31, 1969 No. 15

Skulls of Gymnophiona and Their Significance in the Taxonomy of the Group[1]

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ABSTRACT

The skulls of 48 species and subspecies of Caecilians are reviewed and three photographs of each are presented. Significant differences are demonstrated in the skulls, which would warrant the taxonomic arrangement proposed. Four families are recognized.

INTRODUCTION

Although considerable anatomical study has been done on the skulls of certain genera of the Gymnophiona, skulls of numerous genera are as yet unknown, owing to a dearth of specimens available for such study. I have, with the help of certain museums and individuals, brought together the skulls of nearly four dozen species representing 4 families and 20 genera. For a number of years we have been wont to regard the caecilians as representing a single family and in such case perhaps committing ourselves to the premise that the evolution of the now Gymnophiona has all taken place since they arrived at their present form and habitat. With an examination of the literature descriptions of known species, and the skull studied here, one is convinced that, of the present members of the group, doubtless several had undergone a considerable evolution prior to becoming refugees in subterranean food habitats where competition for food was less severe, and where the loss of limbs and girdles was an adaptation essential to a subterranean existence. Some forms seemingly left the subterranean habitat for a completely aquatic one. It is likewise true that some anatomical studies on the skulls, though excellent, have not been directed in the immediate direction of taxonomy, since the workers were seemingly less concerned with the taxonomic implications than with other aspects.

In my study of caecilians (Taylor, 1968), having utilized such characters as were apparent from preserved specimens (such as body shape, size, folds, scales, proportions and dentition, and, to a lesser extent, reproductive organs, gills, gill slits, eye position, character and position of the tentacle and snout projection, etc.), it became obvious to me that evolution had differentiated the Gymnophiona into several groups of greater significance than genera. Three such groups were considered as families, the Ichthyophidae, Typhlonectidae and Caeciliidae, while a fourth, still little known, likewise appeared that it might be worthy of admission to such a category.

Since this publication appeared, I have proposed that this fourth group be recognized as a new family, the Scolecomorphidae. I have also proposed that the family Caeciliidae, *sensu strictu,* be divided into two subfamilies, the Dermophinae and Caeciliinae (Taylor, 1969b).

The present study was undertaken to ascertain to what extent the gross anatomy of the skull displayed the evolution that was evident in other anatomical areas. Rather than write detailed descriptions of conditions obtaining in each of the skulls, I offer figures, which, in a way, serve as a universal language.

The following abbreviations are used for the names of various collections containing caecilians:

AMNH: American Museum of Natural History, New York, New York.
BMNH: British Museum (Natural History), London, England.
EHT-HMS: Edward H. Taylor-Hobert M. Smith Herpetological Collection, Lawrence, Kansas.
KUMNH: Kansas University Museum of Natural History, Lawrence, Kansas.
MCZ: Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts.
DSBM: Division of Systematic Biology, Museum, Stanford University, Stanford, California.
UIM: University of Illinois Museum, Urbana, Illinois.

THE BONES OF THE SKULLS OF GYMNOPHIONA

Figure 1 is a diagrammatic drawing of a representative gymnophionan skull showing the names of the bones as referred to in this paper.

The skulls of caecilians seem to have undergone a reduction in numbers of bones when compared with many other primitive amphibians, a reduction largely brought about by fusion, or in some cases perhaps by complete loss. For instance the skulls of some generic groups have certain dermal bones which in others are lacking. The usual interpretation is that the missing bones have been fused to surrounding or contiguous bones or that they have "dropped out." One may sometimes trace a bone through a series of related genera to find it diminishing in size until it no longer appears, or, as in the case of the splenial of certain salamanders, it seems as if the bone, with its numerous teeth, is resorbed or eliminated completely during the lifetime of the individual animal.

One common observation of paleontologists and others who treat of skull anatomy is that the earlier geological forms of many groups are very likely to have the greater number of bones; that later forms, usually considered more specialized, have fewer bones. By such a criterion one might consider the family Ichthyophidae as a more primitive group (i.e., retaining more of the primitive characters). However, this would not necessarily bespeak a greater age.

In the Gymnophiona one of the recognized family groups, Ichthyophidae, has pairs of separate dorsal dermal bones, the prefrontals, orbitals (or postfrontals), septomaxillae, premaxillae, and nasals. Two other groups recognized as families, Typhlonectidae and Caeciliidae, lack this series of separate bones. The first three bones are fused to neighboring elements or have dropped out completely. In the case of the nasals and premaxillae, these obviously become fused to form a pair of nasopremaxillae.

The remaining bones of the skull likewise show obvious fusions in all four recognized families. The occipital bones, the otic bones (except stapes) and the otic capsules fuse with the sphenoid bones to form a compound element which is here designated the basisphenoid and serves as the major part of the braincase.

The stapes are present in three of the recognized family groups but are absent in the fourth (Scolecomorphidae).

The maxillary bones are invariably fused to the palatines, and are here called the maxillopalatines, the palatine portion being occasionally referred to as the palatine shelf.

The family Scolecomorphidae has retained the septomaxillae, separate nasals and premaxillae but seeming invariably lacks the prefrontals, the oculars and, strangely enough, the stapes.

The pterygoids are sometimes discernible as separate elements, sometimes they seem to be more or less solidly fused to the quadrate. A tiny ectopterygoid may or may not be present. The quadrate is invariably present, sutured to the squamosal and presenting a surface for the articulation of the lower jaw, as well as a surface or a notch for contact with the stapes (except in the Scolecomorphidae).

The bones of the various groups are fitted together by an overlapping suture or they may be narrowly separated and held together by a cartilage. Sometimes these regions of contact become still more widened by the intervention of musculature. These separations are described as diastemata. One occurs frequently between the squamosal and the parietal. Similarly, the same may happen between the basisphenoid and pterygoid with the palatine shelf of the maxillary. There may be typical sutures, overlapping or interdigitating cartilage covered openings, or there may be very wide diastemata, so that the posterior side walls of the basisphenoids are exposed and the orbitosphenoids, usually not seen, are largely exposed (Scolecomorphidae).

Another variable element is the mesethmoid, which may be completely covered by the dorsal dermal bones or may appear on the dorsal midline of the skull, exposing little or much surface, and serving, often, to separate the frontals, or the nasopremaxillae. Occasionally the anterior part of the parietals may likewise be separated for a distance.

In making the comparisons, I have chosen only a part of the characters. Many others might be mentioned as, for instance, the blood and nerve fenestrae, shape and size of teeth, bone sculpturing, and the internal skull structures. Most of the characters I have used are visible in the cleaned skull without a dissection or dismemberment of the cranium.

Unfortunately, skulls of many of the species are unknown to me or known through only a single skull. Where several skulls of a single species were available, the variation was very meager.

In the Figures, often it is a bit difficult to follow the skull sutures. Perhaps the greatest disappointment is in the teeth. Being at different levels in the skull, rarely are all the teeth in focus at the same time with the magnification used. Moreover, in many of the skulls, many of the teeth are absent, having been lost in the preparation of the skull. Usually the numbers can be counted and their relative size discerned in the skull itself. In the Figures this is not true to the same extent. The reason for this condition is that the teeth are jointed and the distal portions may be lost.

It will be noted that I have not utilized the lower jaws of these specimens in this discussion. The jaws were photographed and studied. The material was on the whole very unsatisfactory inasmuch as the fragile jaws were almost invariably broken in the specimens that had been skeletonized. This was perhaps due to the opening of the closed jaw for the original identification of the species of the preserved specimen. Occasionally, the specimens had been damaged before preservation. The teeth on the lower jaw were often destroyed by the opening of the jaw.

These elements do contribute characters for the differentiation of certain genera and families, but the illustrations, which are most necessary, do not show the characters adequately or at least not to the satisfaction of the author, hence the omission.

DESCRIPTIONS OF SKULLS

Family **Ichthyophidae**

The family characteristics as displayed by the skulls of *Ichthyophis* and *Caudacaecilia* examined are as follows: the number of separate bones is greater than in other known families of the Gymnophiona. Beginning dorsally on the snout tip are the large paired nasals, separated anteriorly by a small wedge formed on the upper tips of the premaxillae; a pair of frontals follow the nasals, and these in turn are followed by a pair of parietals, usually the largest dorsal bones; on each side of the median series are (anteriorly) a septomaxilla bordering the anterior nares, a prefrontal, and an ocular which may be completely free or partially fused to the squamosal; the latter is a large lateral bone. This is preceded by the maxillopalatine, that borders the mouth laterally and reaches forward to contact the premaxillaries, which border the anterior part of the mouth. The posterior part of the skull roof is formed from the sides of the posterior brain case (basisphenoid) which surrounds the large foramen magnum, but the continuity is broken dorsally by a suture in the bone between the foramen and the parietals. Behind the squamosal, and attached to it, is the quadrate. Just posterior to the quadrate is the stapes, whose base serves as part of the brain case wall and sends forward a projection that forms a suture with the quadrate.

The brain case is largely composed of a single compound bone, here designated the basisphenoid, which has incorporated the various occipital, sphenoid and otic bones and possible certain others. It forms a large part of the floor and sides of the brain case and sometimes, in certain families, reaches forward to the prevomerine tooth series. Ventrally there is a constriction of the basisphenoid preceding the otic capsules, anterior to which the bone forms two more or less distinct lateral "wings" which are in contact with the quadrates and the pterygoids. The anterior border of the ventral surface of the skull is formed by the premaxillae and the maxillopalatines. The premaxillae are followed by paired prevomers which are relatively very large in this family, often extending farther back than the internal nares and usually if not always forming a part of their border. The major part of the border of the nares is the palatine shelf of the maxillopalatine. Posteriorly the shelf contacts the pterygoid, which posteriorly joins the quadrate either by suture or in certain cases seemingly by fusion.

The tooth-bearing bones of the skull proper are the premaxillae, the maxillary and palatine sections of the maxillopalatines, and the prevomers. (In certain families where an ectopterygoid is present, it may also bear teeth.) The lower jaws each consist of two compound bones, the dentary, which has incorporated the splenial, and the articulare. In this family this bone bears a series of dentary teeth (usually the largest of all in size) and usually a splenial series (sometimes called the inner mandibular series). This latter may be absent completely in certain families while in other families, including the Ichthyophidae, it may be absent in only some of the genera.

Ichthyophis Fitzinger

Ichthyophis Fitzinger, Neue Classification der Reptilien. . . . Wien, 1826, pp. 36, 63. Type species *Coecilia hypocyanea* van Hasselt.

Fitzinger assigned a single species to this genus. Peters (1879) recognized three species, *Ichthyophis glutinosus* (Linnaeus), *Ichthyophis beddomei* Peters and *Epicrium monochroum* Bleeker. Boulenger, who reviewed the caecilians in 1882, as one of his maiden efforts, placed all Asiatic forms of the genus having a lateral stripe in the species *glutinosus* (Linnaeus); all lacking the stripe in the species *monochrous* (Bleeker).

The genus as now constituted has a large number of forms recognized as species which are confined to southern and southeastern Asia and adjacent island groups. The cranial skeleton is known to me from the skulls of several forms which I recognize as species. This genus differs from the *Caudacaecilia* chiefly in the absence of the splenial teeth in the adult.

Ichthyophis glutinosus (Linnaeus)

(Fig. 2)

Caecilia glutinosa Linnaeus, Systema Naturae . . . , 10th Ed., vol. 2, 1758, p. 229. Type-locality "Habitat in Indiis." It appears to be most probable that the type-locality is Ceylon (see Taylor, 1965).

Data here given are from the skull of KUMNH No. 31291, Tonacumbe Estate, Numunukula, Ceylon.

The general characters agree with those listed for the family and genus. The skull bones show a rather strong overlap on the dorsal surface, the anterior elements overlap the bones behind them and the frontals have two narrowed processes pushing forward between the prefrontals and the nasals. The parietals maintain the same width until they narrow posteriorly. The parietals and squamosals have a very narrow separation, bridged by cartilage; the ocular bone is separate and complete (the bone of this skull figured is broken partially on one side). The septomaxillae border the anterior nasal openings. The tentacular foramen is separate from the orbit but close to it, directed outward and downward rather than forward. The prevomers are not narrowed and not or scarcely separated posteriorly by the spine of the basisphenoid. The pterygoid, which is not fused to the quadrate, sends a narrow process forward that reaches to the internal nares. I do not discern an ectopterygoid and believe it normally absent. The stapes, which has a fenestra through the bone, projects forward into a notch in the quadrate. The "wings" of the basisphenoid are rather poorly developed, and the otic capsules are inflated very little. The tooth rows are subparallel. See Table 1.

Ichthyophis beddomei Peters

(Fig. 3)

Ichthyophis beddomei Peters, Monatsb. Akad. Wiss. Berlin, 1879, p. 932, fig. 4. Type-locality, Nilgherrie Hills, India.

Data given here are from the skull of EHT-HMS No. 3186, Kotegehar, India.

The skull resembles *I. glutinosus* in most characters. The tentacular aperture is somewhat farther forward or, rather, the groove continues farther forward, so that when the tentacle reaches the surface, it is distinctly farther from the eye. The stapes is fenestrated. There are two anterior fenestrae in the prevomers instead of one as in *glutinosus.* See Table 1.

Ichthyophis singaporensis Taylor

(Fig. 4)

Ichthyophis singaporensis Taylor, Univ. Kansas Sci. Bull., 1960, vol. 40, pp. 55-58, figs. 5, 6. Type-locality, Singapore Island.

Data are from the skull of the type-specimen, BMNH No. RR1959.1.2.43. (figured in Taylor, *loc. cit.,* fig. 6).

The ocular bone actually is circular, but on one side the bone tends to fuse to the maxillopalatine. The parietals are notched, constricted near their anterior end, behind which they attain their greatest width. The skull is more compact than in *I. glutinosus,* not or scarcely narrowing anteriorly. The anterior process of the pterygoid is narrower and shorter, not reaching to the level of the internal nares; the squamosals are shorter and wider than in the preceding species. See Table 1.

Ichthyophis kohtaoensis Taylor

(Figs. 5-6)

Ichthyophis kohtaoensis Taylor, Univ. Kansas Sci. Bull., 1960, vol. 40, pp. 110-113, fig. 38. Type-locality, Koh Tao Island, Gulf of Siam.

Data are from the skull of EHT-HMS No. 3935, from about 10 mi. north of Chiang Doi, N. Thailand.

The skull tends to narrow anteriorly as in *I. glutinosus.* The orbit is not completely surrounded by the ocular, and the orbit and the tentacular groove are continuous. The fenestrae, posterior to the internal nares and separating

TABLE 1. Measurements in mm and tooth counts in the skulls of *Ichthyophis*.

Species Number Museum Locality	*glutinosus* 31291 KUMNH Ceylon	*beddomei* 3186 EHT-HMS Mysore, India	*singaporensis* Type BMNH Singapore	*kohtaoensis* 3936 EHT-HMS N. of Chiang Mai, Thailand	*kohtaoensis* 3935 EHT-HMS Chiang Dao, Thailand	*mindanaoensis* 20926 DSBM Misamis, Mind. P.I.
Total length of skull	13.0	11.0	10.4	11.7	13.0	11.5
Greatest width	8.0	7.0	7.0	6.8	8.35	7.4
Width at middle of orbit	6.3	5.5	6.7	?	6.8	6.0
Jaw length	12.2	10.9	10.3	12.0	13.0	11.0
Length of basisphenoid	7.4	6.8	6.5	....	7.5	7.0
Width at "wings"	5.2	4.3	5.0	4.5	5.3	4.7
Width at otic capsules	5.5	5.0	5.0	5.0	5.7	4.8
Length of prevomers	4.5	4.2	3.8	4.0	3.7	4.2
Combined width, prevomers	3.5	3.2	3.7	3.4	3.5	3.0
Length from anterior border of internal nares to condyle	8.4	7.3	5.7	7.5	8.8	7.7
Total length of specimen	320	258	243	?	309	259
Premaxillary teeth	7-8	8-7	7-8	7-7	8-9	7-7
Maxillary teeth	15-15	14-15	16-17	14-17	17-17	17-18
Prevomerine teeth	9-8	11-10	8-6	10-9	9-10	10-10
Palatine teeth	14-15	14-15	13-13	13-15	18-16	16-14
Dentary teeth	?-23	14-?	20-19	24-24	24-26	21-22
Splenial teeth	?-11	14-?	3-3	16-17	17-17	12-11

the pterygoid and basisphenoid, are proportionally larger, and the prevomers are proportionally longer than in *glutinosus.* Table 1 gives data on this and one other skull.

Ichthyophis mindanaoensis Taylor

(Fig. 7)

Ichthyophis mindanaoensis Taylor, Univ. Kansas Sci. Bull., 1960, vol. 40, pp. 69-74, figs. 13-15. Type-locality, Todaya, Mt. Apo, Davao, Mindanao, Philippine Islands. Elev. 2800 ft.

Data are from the skull of DSBM No. 20926, from 11 km. SE of Buena Suerte, on side of Dapitan Peak, Mindanao, P.I. Elev. 3700 ft.

This is similar to the preceding *I. kohtaoensis,* but in this the ocular bone is seemingly fused to the squamosal for much of its region of contact, and the tentacular aperture is separated from the orbit. When the cartilage of the squamosal-parietal suture is removed, there is a very narrow diastema between these bones. The prevomers are shorter than in *I. kohtaoensis.* See Table 1.

Caudacaecilia Taylor

Caudacaecilia Taylor, Caecilians of the World, 1968, p. 165. Type of genus, *Ichthyophis nigroflavus* Taylor.

Taylor referred five species to this genus: *Ichthyophis nigroflavus,* which was designated as type, *I. paucidentulus* Taylor, *I. weberi* Taylor, *I. larutensis* Taylor and *Caudicaecilia asplenia* Taylor. The range of this series of species is spread from the western Philippine Islands through Borneo, Sumatra, and the Malay Peninsula. All differ from *Ichthyophis* in the absence of splenial teeth.

These have the general skull characters of the family Ichthyophidae; that is, the presence of prefrontals, septomaxillae, oculars and separate premaxillae and nasals. The oculars may be partially fused.

The maxillaries and palatines are fused to form the maxillopalatines, and the basisphenoid has incorporated the various occipital and otic bones and the otic capsules to form the basisphenoid that serves as the major part of the brain case. The squamosals, frontals, parietals, quadrates and stapes appear dorsally or laterally; ventrally there are prevomers and pterygoids. The mesethmoid is not visible dorsally.

Skulls are available for four of the five known species as follows:

Caudacaecilia nigroflava (Taylor)

(Fig. 8)

Ichthyophis nigroflavus Taylor, Univ. Kansas Sci. Bull., 1960, vol. 40, pp. 101-103. Type-locality, near Kuala Lumpur ("within 20 miles"), Selangor, Malaya.

The data are from the skull of EHT-HMS No. 1734, Bukit Lagong Forest Reserve, Selangor, Malaya.

The skull is relatively broad, not tapered or tapering but very little anteriorly; the premaxillae are visible dorsally between the nasal openings;

the nasals are narrowed posteriorly; the frontals are nearly as long as the parietals, which widen somewhat posterior to the squamosals. The prefrontals form relatively broad sutures with the septomaxillae. The stapes, partly hidden from above by a shelf of the dorsal part of the basisphenoid, push forward into a rather deep notch in the quadrate. The pterygoids reach to near the edge of the internal nares; no ectopterygoid is present. The orbital rim of eye and the tentacular aperture and groove are continuous. The ocular bones, if considered present, are fused to the squamosals which largely surround the eye. The diastemata following the internal nares are large. The otic capsules are not noticeably inflated. The tooth rows are subparallel, with the inner series extending farther posteriorly than the maxillae. See Table 2.

Caudacaecilia asplenia Taylor

(Fig. 9)

Ichthyophis asplenius Taylor, Univ. Kansas Sci. Bull., 1965, vol. 46, pp. 278-283, figs. 14-15. Type-locality, "Boven Mahakkam," Borneo.

Data are from the skull of EHT-HMS No. 1373, La Doo Tin Mine, Yala Province, Thailand.

This differs from the preceding species in having the orbit almost completely separated from the squamosal by a separate ocular bone, the tentacular aperture distinctly separate from the orbit, and the frontals distinctly shorter than the parietals. The maxillopalatine borders the orbit for a short distance. The skull is slenderer, narrowing more anteriorly than in *C. nigroflava.* On the left pterygoid there are two small teeth (anomaly?). See Table 2.

Caudacaecilia larutensis (Taylor)

(Fig. 10)

Ichthyophis larutensis Taylor, Univ. of Kansas Sci. Bull., 1960, vol. 40, p. 44, figs. 1, 2. Type-locality, Maxwells Hill, Larut Hills, 3380 ft. elev. Perak, Malaya.

Data are taken from the skull of EHT-HMS No. 3359, Topotype.

The ocular, if present, is fused more or less completely with the squamosal. The maxillopalatine is excluded from the orbit and the tentacular aperture is not continuous with the orbit. Dorsally the frontals are as long as or longer than the parietals, with the latter scarcely widening behind the posterior level of the squamosal. The skull tends to be narrower than that of *nigroflava,* especially anteriorly. See Table 2.

Caudacaecilia weberi (Taylor)

(Fig. 11)

Ichthyophis weberi Taylor, Philippine Jour. Sci., 1920, vol. 16, p. 227; type-locality, Malatgan River, Palawan, Philippines. (Type destroyed.)

Data are taken from the skull of DSBM No. 21764. (Paratype of neotype.)

The prevomers are slightly wider posteriorly and do not extend beyond the posterior level of the internal nares; the orbit and the tentacular aper-

TABLE 2. Measurements in mm and tooth counts in skulls of *Caudacaecilia.*

Species Number Museum Locality	*nigroflava* 1734 EHT-HMS Selangor, Malaya	*asplenia* 1373 EHT-HMS Yala, Thailand	*larutensis* 3359 EHT-HMS Perak Malaya	*weberi* 21764 DSBM Palawan, Philippines
Total length of skull	12.0	9.5	11.0	9.0
Greatest width	8.0	6.3	6.8	5.4
Width at orbits	7.4	4.2	6.0	5.0
Length of jaws	12.4	10.5	11.1	8.0
Length of basisphenoid	7.4	6.7	6.2	5.4
Width at "wings"	5.4	4.0	4.2	3.9
Width at otic capsules	5.2	4.3	5.0	4.4
Length of prevomers	4.3	3.3	3.9	3.3
Combined width prevomers	4.4	3.5	3.4	3.15
Front edge of internal nares to condyle	7.9	6.2	7.0	6.0
Length of specimen	385	238	252	209
Premaxillary teeth	11-10	7-8	9-8	8-10
Maxillary teeth	17-15	16-16	19-20	17-17
Prevomerine teeth	13-12	10-10	11-10	11-11
Palatine teeth	15-15	14-15	18-18	13-13
Dentary teeth	18-?	21-21	20-20	20-21
Splenial teeth	0-0	0-0	0-0	0-0

ture are seemingly connected by a narrow groove, and the ocular if present is fused completely to the squamosal. The maxillopalatines border the orbits narrowly. The frontals are shorter than the parietals. The general skull proportions seem to be more similar to *C. nigroflava* than to the other two species. See Table 2.

Family **Typhlonectidae**

The general characteristics of the skull in the Typhlonectidae based on the type genus and *Potamotyphlus* are as follows: The premaxillary and nasal bones are fused and seemingly also have incorporated the septomaxilla. The frontals are largely in contact their entire length, the mesethmoid not visible. The parietals are in contact their entire length. The posterior dorsal portion of the skull is formed by the dorsal part of the basisphenoid, which is sutured above the foramen magnum.

Laterally the maxillopalatine has an anterior opening for the tentacle and posteriorly it surrounds the eye socket for about three fourths of its circumference. This is followed by the squamosal, separated from the parietal by a wide diastema, and bordered posteriorly by the quadrate. There is a small external stapes (this element has been accidentally lost on one side) on the skull of *Potamotyphlus.*

Seen from the ventral surface, the anterior portion of the skull is occupied by the nasopremaxillae. Following this are the two prevomers, bearing the prevomerine teeth on their anterior borders, then narrowing as they extend backward between the huge internal nares, bordering them on their upper anterior edges for about one fifth to one third of their circumference or perhaps more in *Potamotyphlus.*

The lateral portion of the ventral surface is occupied by the maxillopalatine, the palatine portion largely surrounding the internal nares (choanae) and posteriorly separated by an irregular rather narrow diastema from the basisphenoid (partly cartilage covered) or without a noticeable diastema in *Potamotyphlus.* The pterygoid is at least partially fused to the quadrate. The basisphenoid is large with distinct lateral "wings" bordering the pterygoid; it runs forward, and anteriorly as a narrow point, tends to separate the prevomers for a greater or lesser distance (in *T. natans* separated nearly to the prevomerine teeth).

Typhlonectes Peters

Typhlonectes Peters, Monatsb. Akad. Wiss. Berlin, 1879, pp. 930, 940. Type of genus, *Caecilia compressicauda* Duméril and Bibron.

Peters (1879) originally referred four species to the genus: *Caecilia compressicauda* Duméril and Bibron, *Caecilia natans* Fischer, *in* Peters, *Siphonops syntremus* Cope, and *Caecilia dorsalis* Peters.

Of these the first two, *T. compressicauda* and *T. natans* are now recognized in the genus. *Caecilia dorsalis,* a synonym of *Caecilia kaupii* Berthold, is placed in a different genus, *Potamotyphlus;* and *Siphonops syntremus* has likewise been placed in a new genus, *Copeotyphlinus.* Formerly it had been placed in *Typhlonectes* with a ? by Peters, in *Dermophis* by Cope (1866), and treated as *incertae sedis* by Dunn (1942).

Peters recognized the most salient generic features: body lacking scales; eye in an orbit, not covered by bone; tentacular aperture opening close to nostril; splenial teeth present. Both lungs well-developed; foetus with bladder-shaped gills. Aquatic.

Certain other species have been added to the genus: *Thyphlonectes* [sic] *venzuelense* Fuhrman, *Chthonerpeton microcephalum* Miranda-Ribeiro, *Typhlonectes eiselti* Taylor, *Typhlonectes obesus* Taylor, and *Typhlonectes anguillaformis* Taylor. On the authority of Dr. Joseph Bailey, *in* Dunn (1942), *Chthonerpeton microcephalum* is a synonym of *Typhlonectes kaupii*=*Potamotyphlus kaupii* (Berthold).

The skulls of two species of *Typhlonectes* are known to me, *T. compressicauda* and *T. natans.*

Typhlonectes compressicaudus (Duméril and Bibron)

(Fig. 12)

Caecilia compressicauda (Duméril and Bibron), Erpétologie Générale. . . . 1841, vol. 8, p. 278 (type-locality, Cayenne).

The skull is from a specimen, EHT-HMS No. 1731, Belém, Brasil. Since the type came from a different drainage system, one cannot be absolutely certain that this Amazonian population agrees in detail with that from the Guianas.

The characters agree with those of the family: the skulls bones are reduced in number, the prefrontals, septomaxillae, and oculars do not appear, while the premaxillae and nasals are fused to form the two nasopremaxillae. As in all gymnophiones the occipitals, otics, and the otic capsule and sphenoids are fused with the basisphenoid in making the brain case. The palatine and the maxillary are fused; small stapes are present. The pterygoid may be free or fused at least partially to the quadrate. A very small ectopterygoid may be present. The orbits are cut chiefly in the maxillopalatines but are bordered posteriorly by the squamosals; the tentacular aperture notches the anterior part of the same bone, with the groove continuing along the nasopremaxilla. The external narial openings are proportionally large. A wide diastema is present between the parietal and squamosal. The internal nares are of very large size, surrounded, except anteriorly, by the palatine shelf of the maxillary. The prevomers, which border the inner anterior edge, are rather narrowed posteriorly but are separated for about a fourth of their length by the anterior point of the basisphenoid. Seemingly the pterygoid is at least partly fused to the quadrate. The wings of the basisphenoid are distinct. See Table 3.

Typhlonectes natans Fischer, *in* Peters

(Fig. 13)

Typhlonectes natans Fischer, *in* Peters, Monatsb. Akad. Wiss. Berlin, 1879, p. 941. Type-locality, Río Cauca, Colombia.

Data are from the skull of MCZ No. 24524 from "Cúcuta," Colombia.

Compared with the previously described skull, *T. natans* differs in having a proportionately much narrower pair of frontals and still narrower parietals which are less wide than the frontals; the very large diastema between the squamosal and the parietal is as wide as the parietal itself, the greater part of its length. The prevomers have a slight projection anterior to the prevomerine teeth, much narrowed posteriorly and terminating in points posterior to the back level of the nares. These are separated for about two thirds of their length. The pterygoid seemingly is not fused to the quadrate. See Table 3.

Potamotyphlus Taylor

Potamotyphlus Taylor, Caecilians of the World. 1968, pp. 256-257. Type of genus, *Caecilia kaupii* Berthold.

This genus comprises two known species that have the following characters: no scales, no secondaries, head relatively small with a long slender neck, a dorsal skinfold, eyes in sockets, tentacular aperture very close to large

Table 3. Measurements in mm and tooth counts of the skulls of *Typhlonectes* and *Potamotyphlus*.

Species Number Museum Locality	*T. compressicaudus* 1731 EHT-HMS Belém, Brasil	*T. natans* 24524 MCZ Cúcuta, Col.	*P. kaupii* 787 UIM (Uncertain)
Total length of skull	16.5	22.4	11.1
Greatest width	11.2	14.8	5.5
Width at middle of orbits	10	12	5.05
Length of jaw	14.2	21.5	? broken
Length of basisphenoid	11.1	15.5	7.2
Width at "wings"	7.7	8.9	3.5
Width at otic capsules	7.2	8.3	5.0
Length of prevomers	4.8	6.8	3.0
Greatest width of prevomers	4.0	5.0	1.9
Diameter of internal nares	1.8	2.0	2.5
Length of internal nares	3.2	3.2	1.3
Anterior edge of nares to condyle	11.0	15.0	7.2
Premaxillary teeth	9-10	9-9	12-10
Maxillary teeth	15-15	20-20	17-17
Prevomerine teeth	7-5	5-8	4-4
Palatine teeth	19-19	23-20	16-17
Dentary teeth	20-21	21-?	27-27
Splenial teeth	6-6	6-?	6-6
Total length of specimen	432	650	?

nostril, strongly modified body terminus in male serving as a clasper, completely aquatic.

Of the two species known, *P. kaupii* and *P. melanochrus* Taylor (1968), I have been able to study the skull of only the former.

Potamotyphlus kaupii (Berthold)

(Fig. 14)

Caecilia kaupii Berthold Nacht. Gesel. Göttingen, 1859, p. 181. Type-locality, "Angostura"= Ciudad Bolívar, Venezuela.

Data from the skull of UIM No. 787 (locality uncertain).

The diastema between the parietals and squamosals is strong, also separating the squamosal and the frontals for half the length of the latter. The eye socket is between the squamosal and the maxillopalatine, cut chiefly in the latter. The upper edge of the maxillopalatine, bordering the frontal and the nasopremaxilla, is very short, less than half its lower border. In this skull the stapes are absent as they have fallen out while the skull was being prepared, thus accounting for the large opening where the stapes would normally occur. The internal nares are enormously large proportionally, surrounded largely by the palatine shelf of the maxillary. The prevomers are greatly narrowed, with the total distance between the nares about one third of their transverse diameter. The pterygoid is moderate and the ectopterygoids, if present, are very small. Minute diastemata are present posterior to the nares between the palatal shelf and the basisphenoid, the latter remaining wide to near the prevomers but sending forward a spine to separate the prevomers for less than half their length. The suture separating the premaxillary area from the prevomers is transverse, anterior to the prevomerine tooth series. The basisphenoid is but little widened at the poorly developed "wings." The nostrils are large and the large tentacular aperture notches the maxillopalatine. The tentacular groove continues along the nasopremaxilla. See Table 3.

Family **Scolecomorphidae** Taylor

This recently proposed family of the Gymnophiona comprises a single genus with six forms, recognized as species.

In studying the cranial antomy, skulls of two species have been available, *Scolecomorphus vittatus* and *S. kirkii.* Most of the data here recorded are from the former species.

This family retains the premaxillae and the nasals as separate elements, the latter bending down between the nostrils, meeting the premaxillae on the ventral surface of the snout. Of three separate paired bones retained by the *Ichthyophidae* (prefrontals, oculars, and septomaxillae), only the latter are retained. These are short bones partly bordering the nostrils. The maxillae and palatines are fused together as in all Gymnophiona, and are visible both laterally and ventrally. The upper anterior part of the maxillopalatine has an area resembling a prefrontal, but in skulls examined, this area, while of a somewhat different color, is solidly fused with the maxillopalatine.

The nasal bones are large, truncate posteriorly. The frontals form a narrow median suture while their lateral edges are 2.5 times the length of the median suture. The parietals are elongate, sloping downwards in their posterior parts and failing to enter the rim of the foramen magnum by a fraction of a millimeter (0.15 mm). The squamosal and parietal are widely separate, the squamosal attached lightly, and extending farther back than is usual. No stapes are present. The squamosals are lightly attached to the maxillopalatine.

The otic capsules are inflated and solidly fused with the basisphenoid. The prevomers are narrow, slightly widened at the prevomerine tooth series, extending a greater distance in front of the teeth than they do behind them. No eye sockets are present. The tentacular apertures are large, opening in the maxillopalatines, and extending forward, the grooves not covered by bone, widening considerably anteriorly. The internal nares are surrounded by the orbitosphenoid and partially by the palatine shelf of the maxillopalatine. This latter shelf, bearing the palatine teeth, is directed diagonally outwards so that the back part of this dental series comes to lie in a line behind the maxillary teeth, and thus widely separated from the basisphenoid. A very wide diastema is present between the basisphenoid and the palatine shelf, thus exposing the orbitosphenoid, which tends to reach up to the dorsal skull surface. The basisphenoid forms the lateral part of the brain case. There is a wide diastema between the prevomerine teeth and the palatine teeth. I have not discerned ectopterygoids. The pterygoids seemingly are fused to the quadrates. The splenial teeth are absent.

Scolecomorphus (Boulenger)

Scolecomorphus Boulenger, Ann. Mag. Nat. Hist., ser. 5, vol. 11, 1883, p. 48. Type of genus *Scolecomorphus kirkii* by monotypy. The type-locality thought to be probably "Lake Tanganyika."

Scolecomorphus vittatus (Boulenger)

(Fig. 15)

Bdellophis vittatus Boulenger, Proc. Zool. Soc., London, 1895, p. 412, pl. 24, fig. 4. Type-locality, Usambara Mountains, Tanganyika (Tanzania).

Data are taken from the skull of EHT-HMS 4642, from Nyange, Kenya.

For the general skull description, see the preceding family description and Table 4.

The genus *Bdellophis* was erected by Boulenger for a caecilian presumably differing from *Scolecomorphus* in having the eye not covered by bone

TABLE 4. Measurements in mm and tooth counts of skulls of *Scolecomorphus*.

Species	*vittatus*	*kirkii*	*kirkii*	*kirkii*
Number	4642	27120	27106	27116
Museum	EHT-HMS	MCZ	MCZ	MCZ
Locality	Nyange, Vituri, Tanzania	Cholo Mts., Malawi	Cholo Mts., Malawi	Cholo Mts., Malawi
Greatest length of skull	7.25	7.9	7.2+	7.4
Greatest width	3.7	4.05	4.0+	?
Jaw length	5.9	6.0	6.0	?
Length of basisphenoid	4.8	5.35	broken	5.3
Width at otic capsules	2.5	3.0	3.+	3.1
Length of the prevomers	1.75	1.9	1.85	2.1
before prevomerine teeth	0.9	1.0	1.0	1.2
behind prevomerine teeth	0.55	0.7	.65	.09
Combined width, greatest	1.0	1.15	1.1	1.2
Length, anterior part of internal nares to condyle	4.8	5.3	?	5.3
Length of specimen, total	230±	270	?	?
Premaxillary teeth	2-3	3-3	3-2	3-3
Maxillary teeth	6-6	8-7	8-?	....
Prevomerine teeth	2-3	4-3	3-3	2-3
Palatine teeth	7-6	7-7	....	....
Dentary teeth	13-?	12-?	?-13	....
Splenial teeth	0-0	0-0	0-0	0-0

(but not in a socket). Barbour and Loveridge (1928), seemingly not examining the skull carefully, state "An examination of the skull of a topotypic specimen of *B. vittatus* shows that the character of 'eyes distinct,' which separates the genus from *Scolecomorphus* whose eyes are below the cranial bones, is a sign of youth." I have not been able to verify this statement.

I did examine the type in London and from notes taken I read "The eye is very far forward, not under bone, nor in an orbit, but carried by the tentacle from under the bone into the tentacular trough, which for much of its length is not bone-covered." In many specimens the eye may be seen dimly through the skin at the base of the tentacular aperture or just under the nostril.

Scolecomorphus kirkii Boulenger

(Fig. 16)

Scolecomorphus kirkii Boulenger, Ann. Mag. Nat. Hist., ser. 5, vol. 11, 1883, p. 48. Type-locality uncertain; thought to be presumably in the region of Lake Tanganyika (Tanzania).

Data are from the skulls of MCZ 27120, MCZ 27106 and MCZ 27116, all from the Cholo Mountains, Malawi.

The specimens of the skulls available and the photographs leave much to be desired. They are fragile and the differences between *S. vittatus* and *S. kirkii* as displayed in the Figures are not great. They seem to agree in all family characters. In two of the specimens the eyes were discovered imbedded in the tentacles in the anterior part of the tentacular grooves. A detailed description of the skulls may be found in Taylor (1969). See Table 4.

Family **Caeciliidae**

The prefrontals, oculars and septomaxillae are absent as separate bones while the nasals and premaxillae are fused to form the two nasopremaxillae. Usually the frontals are completely separated by the mesethmoid in the subfamily Caeciliinae (one exception may be *C. tentaculata*), but it is not generally true of the Dermophinae. Thus the genus *Dermophis* has at least one species with the frontals separated; some species with the frontals partly separated and some without an external trace of the mesethmoid. *Geotrypetes* has at least one species with the frontals completely separated and one incompletely separated. The skulls of the species seen of *Uraeotyphlus, Gegeneophis, Afrocaecilia* and *Grandisonia* have no external trace of the mesethmoid on the dorsal surface of the skull. In *Boulengerula, Schistometopum* and *Siphonops* the mesethmoid completely separates the frontals. (The other three families show no trace of the mesethmoid dorsally in the species here studied.)

This family is treated under the two subfamilies, Caeciliinae and Dermophinae.

Subfamily **Caeciliinae**

The significant characters of the two genera included in this subfamily are the longer and heavier teeth, and the anterior processes on the prevomers notching the nasopremaxillaries. Also, one group of species has a well-defined eye socket, the other group has the eye solidly roofed over with bone.

In this subfamily the tentacular opening appears almost directly below the nostril, usually about the same distance from the nostril and edge of the lip and concealed by the snout so as not to be visible from above.

Caecilia Linnaeus

Caecilia Linnaeus, Systema Naturae, 1758, Ed. 10, vol. 1, p. 229. Type of genus, *Caecilia tentaculata* Linnaeus (by monotypy).

This genus now has a large number of species all confined to southern Central America and South America.

Skulls of seven species have been available. The skull characters are given in greater detail for the species *C. nigricans,* than for the others. This is one of the largest members of the genus and in fact of all Gymnophiona.

Caecilia nigricans Boulenger

(Fig. 17)

Caecilia nigricans Boulenger, Ann. Mag. Nat. Hist., ser. 7, 1902, vol. 9, p. 51. Type-locality, Río Lita, N. W. Ecuador or southwest Colombia (3000 feet).

Data here recorded are chiefly from the skull of KUMNH No. 94377 from Darién, Panamá.

Two other forms, described by Boulenger (1913), *Caecilia intermedia* and *Caecilia palmeri,* from Ecuador and Colombia respectively, have been placed as synonyms of this species.

This skull displays the family characters of the reduced number of dorsal dermal bones with the usual fusions. The parietals are sharply declivous posteriorly, while anteriorly two median processes push forward separating the posterior parts of the frontals and contacting the narrow mesethmoid which is between the frontals. The very small orbits of the eyes are cut in the maxillopalatines anterior to the squamosal border; the squamosal bones are wider but shorter than the maxillopalatines; the tentacular aperture is at the anterior end of the maxillopalatine, with the groove extending along the side of the nasopremaxilla for some distance. No diastemata are present between the parietals and squamosals and the stapes are seemingly more posterior than is usual.

On the ventral surface of the skull the prevomers, which have flattened projections anterior to the prevomerine tooth series, are longer than their combined width, and are separated posterior to the tooth series for four fifths of their length by a narrow pointed spine of the basisphenoid. The premaxillary tooth series is widely separated from the prevomerine teeth.

The internal nares are bordered on their inner edges by the prevomers, elsewhere by the palatine shelf of the maxillopalatine. A diastema exists between the basisphenoid, pterygoid process, and the palatine shelf, the opening being about double the size of a naris. The "wings" of the basisphenoid are prominent, tending to bend down, leaving the basisphenoid somewhat domed as seen from below; the otic capsules are not or are scarcely inflated; no ectopterygoid is discernible, and the pterygoids do not reach to the internal nares. The transverse bosses below the otic capsules are prominent. See Table 5.

Caecilia tentaculata Linnaeus

(Fig. 18)

Caecilia tentaculata Linnaeus, Systema Naturae, Ed. 10, vol. 1, 1758, p. 229. Type-locality "America"=Surinam (see the earlier description by Linnaeus which preceded the 10th edition).

Data are chiefly from the skull of KUMNH No. 104438, Santa Cecilia, Napo-Pastaza, Ecuador.

Caecilia ithmica, described by Cope (1887) from Darién, appears to be a synonym of this species. *Amphiumophis andicola* Werner from Chanchamayo, Perú has been referred to this species also, but of this I am not certain, not having yet been able to examine the type. *Caecilia albiventris* Daudin also has been synonymized with *C. tentaculata,* but after examination of a skull I regard this as a legitimate species (see later discussion).

Although this specimen is about 200 mm shorter than the *C. nigricans* described, the skull is higher, longer and tapers more toward the snout. The eye is cut into the maxillopalatine farther from its posterior end. The parietals are shaped much the same but are more narrowed at the posterior end and the mesethmoid does not complete the separation of the frontals and consequently does not separate the posterior parts of the nasopremaxillae. The pterygoid (seemingly fused to the quadrate) is shorter and wider than that in *C. nigricans.* See Table 5.

Caecilia degenerata Dunn

(Fig. 19)

Caecilia degenerata Dunn, Bull. Mus. Comp. Zool., Harvard College, 1942, vol. 91, pp. 505-508. Type-locality, Garagoa, Cundinamarca, Colombia.

Data are from the skull of a paratype, AMNH No. 23354, "Colombia," without a specific locality.

All the bones of this specimen are greenish, not impossibly caused by the method of preservation. This is a much smaller species than *tentaculata* but the arrangement of the dorsal bones of the skull are much the same. The orbit is proportionally even larger; the maxillopalatine is slightly longer proportionally. See Table 5.

TABLE 5. Measurements in mm and tooth counts of the skulls of *Caecilia*.

Species	*nigricans*	*tentaculata*	*degenerata*	*disossea*	*volcani*	*orientalis*	*albiventris*
Number	94377	104438	23354	1808	4696	4677	49960
Museum	KUMNH	KUMNH	AMNH	EHT-HMS	EHT-HMS	EHT-HMS	AMNH
Locality	Cana, Darién	Santa Cecilia, Napo-Pastaza	Colombia	Río Cararay, Ecuador	Antón, Panamá	"Ecuador"	Bogotá, Colombia
Total skull length	21.0	24.0	10.4	6.9	8.5	9.0	10.3
Greatest width	13.2	16.0	5.8	3.8	5.1	5.2	5.9
Width at orbit	11.6	13.0	4.7	3.0	4.15	4.3	4.75
Jaw length	19.0	20.5	8.0	4.9	7.0	7.1	8.1
Length of basisphenoid	15.0	15.7	6.3	4.2	5.6	5.6	7.7
Width at wings	8.7	10.0	4.0	2.4	3.4	3.6	4.0
Width at otic capsules	9.9	9.0	3.7	3.0	3.5	4.05	4.4
Length of prevomers	6.8	9.1	3.0	2.0	2.5	2.75	3.0
Combined width	6.2	5.1	2.3	1.4	1.9	2.2	2.0
Length anterior part of nares to condyle	12.5	14.4	6.0	4.2	5.7	6.0	6.85
Total length of specimen	1004	790	350	686	290	337	278
Premaxillary teeth	3-4	3-4	4-4	4-3	4-3	3-4	3-3
Maxillary teeth	9-9	8-8	5-4	6-6	6-6	8-9	7-7
Prevomerine teeth	4-4	3-3	3-3	3-4	3-4	3-4	3-3
Palatine teeth	8-8	7-9	7-7	6-6	5-5	9-10	8-8
Dentary teeth	12-13	13-13	10-10	9-9	11-11	10-11	9-?
Splenial teeth	3-3	2-2	2-2	2-2	1-1	2-2	3-?

Caecilia disossea Taylor

(Fig. 20)

Caecilia disossea Taylor, Caecilians of the World, 1968, pp. 374-378, figs. 196-197. Type-locality, mouth of the Río Santiago, Perú (a river rising in southern Ecuador, flowing into the Río Marañon).

Data are taken from the skull of EHT-HMS No. 1808, from "Alto Cararey Napo-Pastaza, Ecuador."

This is a very elongate, slender species. The mesethmoid separates the frontals but does not enter between the posterior parts of the nasopremaxillae. The orbit of the eye is well-defined. The median points of the parietals separate the posterior part of the frontals slightly. See Table 5.

Caecilia volcani Taylor

(Fig. 21)

Caecilia volcani Taylor, Univ. Kansas Sci. Bull., 1969, vol. 48, pp. 315-323, figs. 1-4. Type-locality, Valle de Antón, Panamá.

Data are recorded from the skull of EHT-HMS 4696, topotypic paratype.

The mesethmoid separates the frontals and pushes forward between the nasopremaxillae slightly; the parietals have two short median prongs that touch the mesethmoid. There is a fine suture from the orbit to the frontal and one from the orbit to the tentacular aperture. Thus the eye is between a large upper portion and a lower portion of the maxillopalatine. This may be an anomalous condition since it is the only known member of this family that I have seen having such an arrangement. The two parts seem to be fused solidly with the maxillopalatine. See Table 5.

Caecilia orientalis Taylor

(Fig. 22)

Caecilia orientalis Taylor, Caecilians of the World, 1968, pp. 417-425, figs. 220-224, 224a. Type-locality, La Bonita, Napo-Pastazo prov., elev. 6300 ft. Ecuador.

Data are from the skull of EHT-HMS No. 4677, from "Ecuador."

The mesethmoid is minute, separating the frontals completely; the prevomers reach back to the posterior level of the internal nares; the pterygoids reach forward to practically the same level. See Table 5.

Caecilia albiventris Daudin

(Fig. 23)

Caecilia albiventris Daudin, Histoire naturelle, générale et particulière des reptiles. . . . 1803, pp. 423-426, pl. 92, fig. 1 (not fig. 2 as stated). Type-locality, "Surinam."

Data are from the skull of AMNH No. 49960, "Bogota," Colombia.

I am resurrecting this name from the synonymy of *Caecilia tentaculata* Linnaeus. The skull of the species differs from that of *C. tentaculata* in being longer and slenderer proportionally; the eye socket is larger, and the stapes is somewhat differently shaped; seemingly the nostril is proportionally much larger. See Table 5.

Oscaecilia Taylor

Oscaecilia Taylor, Caecilians of the World, 1968, p. 598. Type by designation, *Caecilia ochrocephala* Cope.

Taylor referred six species to this genus as follows: *Caecilia ochrocephala* Cope (1866); *C. polyzona* Fischer *in* Peters (1879); *C. elongata* Dunn (1942); *C. bassleri* Dunn (1942); *Oscaecilia hypereumeces* Taylor (1968); and *O. zweifeli* Taylor (1968). Of these, *O. polyzona,* known from three specimens, is a close relative of *O. ochrocephala. C. elongata* is problematical since the poorly described type and typotypic paratype have been destroyed, and one fragmentary specimen, also referred to the form, is seemingly not a member of the species. It unfortunately lacks the head and the anterior part of the body; the posterior part differs from the type in certain recorded characters.

These species appear to be more closely related to *Caecilia* and they differ so much from the remainder of the genera recognized in the family Caeciliidae that I have proposed that these two genera be placed in a distinct subfamily.

Oscaecilia ochrocephala (Cope)

(Figs. 24-25)

Caecilia ochrocephala Cope, Proc. Acad. Nat. Sci. Philadelphia, 1866, vol. 18, p. 132. Type-locality, Atlantic side, Isthmus of Darién, Panamá.

The data here recorded are from the skull of MCZ No. 14817, from Ancón, Canal Zone, Panamá.

For a considerable time this species was regarded a member of the African genus *Herpele,* which association seemingly is wholly unjustified.

The narrow mesethmoid separates the frontals completely and runs forward to separate the posterior parts of the nasomaxillae and posteriorly to separate the anterior prongs of the parietals. The squamosal is short (2.6 mm), the maxillopalatine being much longer (4.6 mm). No diastemata are present between the parietals and squamosals.

The snout projects considerably beyond the mouth, its anterior edge presenting a sharp transverse edge; the under surface of the projection is smooth and flat. The teeth of the premaxillaries and anterior maxillaries are large with very thick bases. The prevomers have an anterior flattened area preceding the prevomerine teeth; posteriorly they reach considerably behind the posterior level of the posterior nares, and are separated by a spine from the basisphenoid, which overlays the inner edges of the prevomers. The nares are largely surrounded by the palatine shelves of the maxillaries, the remainder by the prevomers.

The pterygoids are narrow and elongate, seemingly fused to the quadrates posteriorly. No ectopterygoids are apparent. The "wings" of the basisphenoid tend to turn down, leaving the posterior ventral surface somewhat domed (seen from below). A strong transverse boss is evident below the

TABLE 6. Measurements in mm and tooth counts of skulls of *Oscaecilia.*

Species	*ochrocephala*	*ochrocephala*	*bassleri*
Number	14817	41092	4675
Museum	MCZ	UIM	EHT-HMS
Locality	Ancón, Canal Zone	Gatun, Canal Zone	Ecuador
Total length	12.1	8.9	9.0
Greatest width	6.6	5.2	4.8
Jaw length	9.5	6.25	broken
Length of basisphenoid	8.6	5.7	5.6
Width at wings	3.55	3.3	3.2
Width at otic capsules	4.0	3.5	3.4
Length of prevomers	4.2	2.5	3.0
Combined width anterior border internal nares to condyle	7.2	5.0	5.15
Total length of specimen	542±	?	890±
Premaxillary teeth	3-2	2-3	4-3
Maxillary teeth	5-6	5-4	9-9
Prevomerine teeth	5-4	4-3	4-3
Palatine teeth	8-7	7-8	8-8
Dentary teeth	11-12	10-11	11-11
Splenial teeth	4-4	3-3	3-3

otic capsule. This capsule is scarcely inflated. The stapes makes a rather widened contact with the quadrate. The tentacular apertures are visible from a ventral view of the skull.

A second skull, EHT-HMS No. 1810, from Gatun, Canal Zone, Panamá differs in no essential detail, though it is smaller. See Table 6.

Oscaecilia bassleri (Dunn)

(Fig. 26)

Caecilia bassleri Dunn, Bull. Mus. Comp. Zool. Harvard College, 1942, vol. 91, p. 518. Type-locality, Río Pastaza, Ecuador.

The data here recorded are from the skull of EHT-HMS No. 4675, from Ecuador.

Unfortunately the type series of *C. bassleri* contains specimens of two species, *Oscaecilia bassleri* and *Caecilia disossea.* This has led to much confusion.

The character of the mesethmoid is quite similar to that of *O. ochrocephala* save that the forward prongs of the parietals are scarcely developed; there is no orbit, but the position of the eye is dimly visible through the semitransparent bone of the maxillopalatine. The area of contact of the stapes with the quadrate is smaller proportionally. The tentacular apertures are visible from the ventral face of the skull. The spine of the basisphenoid overlays the edges of the posterior projections of the prevomers. The forward projection of the snout has a rounded rather than a sharp tip in lateral view. See Table 6.

Subfamily **Dermophinae**

The Dermophinae have the general characteristics of the Caeciliidae but lack the characteristic distinguishing features of the Scolecomorphidae, Typhlonectidae and the Ichthyophidae. From the subfamily Caeciliinae, they differ in lacking the relatively large teeth, the tentacular aperture is never as far forward as the nostril, and there is a strong reduction in the range of the numbers of vertebrae. The tentacular aperture is in the maxillopalatine and seemingly never emerges from under the anterior edge of the bone.

The genera included in this subfamily show a considerable differentiation on the generic level, and future studies may provide data that would suggest the presence of other subfamily groups. Probably the most aberrant genus is *Idiocranium*, comprising only a single known species.

Dermophis Peters

Dermophis Peters, Monatsb. Akad. Wiss. Berlin, 1879, p. 937, fig. 6. Type of genus: *Siphonops mexicanus* Duméril and Bibron.

Peters (1879) assigned a series of species to this genus without designating a type. One, however, was named by G. N. Noble (1924) who designated *D. mexicanus* as the type. The species originally placed in the genus were *Siphonops mexicanus* Duméril and Bibron, *S. brevirostris* Peters, and four questioned species: *S. thomensis* Barboza du Bocage, *S. brasiliensis* Lütken, *S. proximus* Cope and *S. simus* Cope.

Of these species only the first is retained in the genus; the others are treated under other genera. Thus *S. brevirostris* and *S. thomensis* are recognized in *Schistometopum* Parker; *S. proximus* in *Gymnopis* Peters; *S. simus* in *Cryptopsophis* Boulenger; and *S. brasiliensis* in *Luetkenotyphlus* Taylor.

Several other forms, species or subspecies, have, however, been added to the genus *Dermophis* by Taylor (1968). These are *Gymnopis oaxacae* Mertens, *Dermophis occidentalis* Taylor, *Gymnopis parviceps* Dunn, *Dermophis balboai* Taylor, *Dermophis glandulosus* Taylor, *Dermophis eburatus* Taylor, *Dermophis septentrionalis* Taylor, *Gymnopis gracilior* Günther; and *Gymnophis* [sic] *clarki* Barbour as a subspecies of *Dermophis mexicanus*.

Dermophis is readily separated from *Gymnopis* by two well-defined generic characters: the eye appears in an open socket, externally visible, and the splenial teeth are lacking. *Gymnopis*, on the other hand, has the splenial teeth and there is no orbit, the eye being covered by bone. There are certain other differences as well.

Both of these genera are largely confined to Central America, only two known forms of *Dermophis* entering South America.

The species of the genus have the following characters: secondary folds present; scales present; three series of teeth (the splenials absent); parietals and squamosals forming sutures; tentacle closer to eye than to nostril; eye in a socket, not covered by bone. Large and small species occur.

Skulls of several species are illustrated. That of *Dermophis eburatus* is described more at length; the other species illustrated are compared to it to point out differences that exist.

Dermophis eburatus Taylor

(Fig. 27)

Dermophis eburatus Taylor, Caecilians of the World, 1968, pp. 473-475, figs. 252, a, b, c, d, e; type-locality, "Nicaragua."

The data are taken from the skull of MCZ No. 12121, from Guatemala, C.A.

This species agrees in the basic family characters, lacking separate prefrontals, septomaxillae and orbitals, and having the premaxillae fused to the nasals to form nasopremaxillae. The frontals are normal but posteriorly they are partially separated by the mesethmoid, which is very narrow.

The squamosal is widened posteriorly, thus narrowing the parietal near its middle, but it widens considerably posterior to the squamosal. The outer posterior edges of the squamosal are slightly elevated above the jaw condyle, leaving a cavelike overhang for muscle attachment. The stapes, much widened, is widely overhung by a free edge of the dorsal basisphenoid, which conceals much of the bone from a dorsal view. The orbit is largely in the anterior part of the squamosal but is bordered anteriorly by the maxillopalatine; the tentacular aperture is relatively large near the anterior end of the maxillopalatine, not forming an anterior groove. The two upper dental series are subparallel. The compound basisphenoid bone has a sharp anterior spine that separates the prevomers for most of their length; the internal nares are largely surrounded by the palatine shelf; however, the prevomers border them on the anterior inner border for a short distance. The nares are elevated above the remainder of the palate (the skull seen from its ventral face); the pterygoid, seemingly, is partly fused to the quadrate, and an ectopterygoid is not discernible. The otic capsules are not swollen, but below the area two strongly developed outer transverse bosses are evident. See Table 7.

(All the bones, skull, jaws, vertebrae, and ribs of this specimen are a dark reddish brown. I presume that this is due to some chemical used in preservation.)

Dermophis costaricensis Taylor

(Fig. 28)

Dermophis costaricense Taylor, Univ. Sci. Bull., 1955, vol. 37, pp. 506-509, fig. 2, Photo. (Type locality, Cinchona [Isla Bonita], Heredia Province, C. R. at near 4000 ft.)

Data are from the skull of KUMNH No. 66805.

This resembles the preceding skull of *D. eburatus* but with the following differences: the mesethmoid is evident between the anterior part of the frontals and is shorter. The parietals are but slightly constricted mesially, and the squamosals are less widened posteriorly. The free edge of the dorsal part of the basisphenoid hides much less of the stapes, while the free outer posterior edge of the squamosal makes a very slight cavelike indentation above the jaw condyle. The otic capsules are slightly more inflated. See Table 7.

Dermophis balboai Taylor

(Fig. 29)

Dermophis balboai Taylor, Caecilians of the World, 1968, pp. 461-467, figs. 244-248. Type-locality, Tacarcuna, Darién, Panamá.

Data are taken from the skull of KUMNH No. 108935.

This is similar to *D. eburatus* but the mesethmoid is visible only as a narrow mesial line the entire length of the frontals, widening slightly anteriorly; the maxillopalatines border on the orbits for a greater distance; the stapes resemble those of *D. eburatus* more than those of *D. costaricensis.* The parietals are narrowed and the posterior part of the squamosals are as wide as in *D. eburatus.* See Table 7.

Dermophis parviceps (Dunn)

(Fig. 30)

Siphonops parviceps Dunn, Occ. Papers, Boston. Soc. Nat. Hist., 1924, vol. 5, pp. 93-94. Type-locality, La Loma (1200 ft.), Boco del Toro Province, Panamá.

Data are taken from the skull of KUMNH No. 36276.

There is no evidence of a mesethmoid. On the ventral surface the most striking character is that the palatine shelf of the maxillopalatine *completely surrounds the nares, the rim of which is unbroken;* the separation of the prevomers is marked by a rather strong ridge, the most elevated part being the spine of the basisphenoid. The parietals are only slightly constricted mesially. Only the inner edge of the stapes is hidden when seen from above. See Table 7.

Dermophis glandulosus Taylor

Dermophis glandulosus Taylor, Univ. Kansas Sci. Bull., 1955, vol. 37, pp. 509-511, fig. 3. Type-locality, San Isidro del General, San José Prov., Costa Rica.

Data are from the skull of KUMNH No. 56070, San Isidro del General, San Jose, C.R.

This skull has the mesethmoid well developed, completely separating the frontals. The parietals are only slightly narrowed. In contrast to *D. parviceps,* the posterior part of the prevomers is wider and with a concommitant widened space between the internal nares. The dorsal bones of the skull show a strong overlap anteriorly. See Table 7.

Dermophis occidentalis Taylor

(Fig. 32)

Dermophis occidentalis Taylor, Univ. Kansas Sci. Bull., 1955, vol. 37, pp. 503-506, fig. 1.

Data are from the skull of KUMNH No. 36296, topotypic paratype.

TABLE 7. Measurements in mm and tooth counts of skulls of *Dermophis*.

Species	*eburatus*	*costaricensis*	*balboai*	*parviceps*	*glandulosus*	*occidentalis*	*m. mexicanus*
Number	12121	66805	108935	36276	56070	36296	66889
Museum	MCZ	KUMNH	KUMNH	KUMNH	KUMNH	KUMNH	UIM
Locality	Guatemala	Moravia Cartago, Costa Rica	Darién, Panamá	Moravia Cartago, Costa Rica	San Isidro, C.R.	between San Isidro & Dominical, Costa Rica	Chiapas, México
Total length	20.0	13.5	14.05	8.2	8.85	6.75	16.3
Greatest width	14.5	8.5	9.5	5.0	6.4	4.0	10.6
Width at orbit	12.0	7.0	7.9	4.0	4.5	3.35	8.4
Length of jaws	18.5	?	12.1		7.0	5.1	14.3
Length of basisphenoid	16.5	11.2	11.5	6.25	7.5	5.0	10.8
Width at wings	7.7	4.8	5.2	3.0	3.5	2.1	6.0
Width at otic capsules	8.4	5.2	6.0	4.0	4.0	2.8	6.5
Length of prevomers	5.5	3.7	3.3	2.0	1.7	1.5	4.2
Combined width	6.7	4.1	4.0	2.05	2.1	1.9	4.9
Anterior border of internal nares to condyle	12.6	9.0	9.5	5.0	5.8	4.5	11.0
Total length of specimen	419	344	356	193	180	194	402
Premaxillary teeth	8-9	7-8	6-6	6-6	6-5	6-5	7-8
Maxillary teeth	13-13	14-2	12-11	8-10	8-7	8-8	11-11
Prevomerine teeth	9-9	9-10	6-5	6-6	6-6	6-6	8-8
Palatine teeth	14-13	16-16	15-14	11-11	11-10	8-7	11-10
Dentary teeth	18-18	....	14-14	12-12	12-11	10-11	14-13
Splenial teeth	0-0	0-0	0-0	0-0	0-0	0-0	0-0

The constriction of the parietals anterior to their middle is rather pronounced. The frontals are proportionally shorter than in previous species. The maxillopalatines form as much of the orbit as the squamosal. The posterior part of the prevomers is narrower. See Table 7.

Dermophis m. mexicanus (Duméril and Bibron)

(Fig. 33)

Siphonops mexicanus Duméril and Bibron, Erpétologie générale. . . . 1836, pp. 284-285. Type-locality "Mexico."

Data are from the skull of UIM No. 66889, Chiapas, México.

The narrow mesethmoid separates the rather elongate frontals for about half their length. The posterior parts of the prevomers are not especially narrowed. The stapes is proportionally less covered by the dorsolateral edge of the dorsal part of the basisphenoid; the transverse bosses below the otic capsules are prominent. See Table 7.

Gymnopis Peters

Gymnopis Peters, Monatsb. Akad. Wiss. Berlin, 1874, p. 616, pl. 1, fig. 1. Type of the genus, *Gymnopis multiplicata* Peters.

Peters described this genus very briefly as follows: "Augen nicht von der Haut überzogen, frei, keine Gesichtsgruber." Only the type was included. Other distinguishing characters are: splenial teeth, secondaries, and scales present. Eye covered by bone. The tentacle is nearer to the commissure of the jaws than to the nostril.

A number of other species have been treated in the genus by Dunn (1942) as follows: *Siphonops proximus* Cope, *Rhinatrema unicolor* A. Duméril, *Siphonops oligozonus* Cope, *Gymnopis multiplicata oaxacae,* Merters, *Gymnophis* [sic] *nicefori* Barbour, *Dermophis albiceps* Boulenger, *Gymnophis* [sic] *clarki* Barbour, *Dermophis gracilior* Günther, and *Siphonops parviceps* Dunn. Dunn later (1944, 1945) described *Gymnopis pricei* and *Gymnopis braziliensis.* Gorham (1962) also referred *Dermophis costaricensis* Taylor, *Dermophis glandulosus* Taylor and *Dermophis occidentalis* Taylor to the genus *Gymnopis!*

Of this list of species only *Gymnopis multiplicata, G. proxima* and *G. oligozona* agree in having the essential characters of the genus, and only these are recognized by Taylor (1968). The other species mentioned are considered as belonging to other genera.

The skull characters are known to me by three specimens: one of *G. proxima* and two of *G. multiplicata.* (Since these two rather closely related forms appear to be separated without direct evidence of integradation, I am treating them as species rather than subspecies.)

Gymnopis multiplicata Peters

(Fig. 34)

Gymnopis multiplicata Peters, Monatsb. Akad. Wiss. Berlin 1874, p. 616, pl. 1, fig. 1. Type-locality, Veragua, Panamá.

Data are recorded from two skulls from Guanacaste, C.R., EHT-HMS No. 4702, and KUMNH 117457, but mostly from the latter.

The prefrontals, septomaxillae, and oculars do not appear as separate bones and the premaxillae and nasals are fused to form the nasopremaxillae. The mesethmoid is visible mesially at the junction of the nasopremaxillae and the frontals. The eye is without socket, bone covered, but is visible under the anterior part of the squamosal. The aperture of the tentacle is subcircular, cut in the maxillary, and not forming a forward-directed open groove. The stapes is present, large, and the bone seemingly not fenestrated. Ventrally the internal nares are somewhat narrowed, definitely diagonally placed and surrounded almost completely by the palatine portion of the maxillopalatine, although the prevomer borders the inner anterior edge for a very short distance. The prevomers are narrowly separated for more than four fifths of their length by a forward-projecting spine of the basisphenoid. A very narrow diastema follows the nares, between the basisphenoid and the palatine shelf. The tooth rows are nearly parallel. An ectopterygoid is present! The second skull differs in no significant point from the one described. See Table 8.

TABLE 8. Measurements in mm and tooth counts of the skulls of *Gymnopis*.

Species Number Museum Locality	*multiplicata* 4702 EHT-HMS Guanacaste, C.R.	*multiplicata* 117457 KUMNH Guanacaste, C.R.	*proxima* 4712 EHT-HMS Turrialba, C.R.
Total length of skull	16.0	14.5	16.85
Greatest width	10.8	9.7	11.6
Length of jaw	16.0	13.7	15.7
Length of basisphenoid	13.65	12.6	11.6
Width at wings	5.9	5.1	6.3
Width greatest posteriorly	7.0	6.0	6.7
Length of prevomers	4.7	4.0	4.5
Combined width, greatest	5.0	4.1	5.0
Anterior edge of choanae to condyle	11.0	9.2	11.8
Premaxillary teeth	10-10	11-8	10-9
Maxillary teeth	14-15	12-12	16-16
Prevomerine teeth	10-10	7-8	9-9
Palatine teeth	15-16	14-13	20-19
Dentary teeth	19-20	16-16	20-20
Splenial teeth	1-1	1-1	1-1
Length of preserved animal	430	?	459

Gymnopis proxima Cope

(Fig. 35)

Siphonops proximus Cope, Proc. Amer. Phil. Soc. 1877, vol. 17, p. 90. Type-locality, "Eastern Costa Rica."

Data are from the skull of EHT-HMS 4712, from Turrialba, C.R.

This skull is similar to that of the preceding species but the following characters obtain: the prevomers do not border the internal nares, they are separated by the basisphenoid for about two fifths of their length only. The diastema (fenestra) between the basisphenoid and the palatine shelf of the maxillary is a little larger. The anterior narrowed portion of the *stapes is fenestrated near to the point of contact with the quadrate.* The eye is visible under the anterior edge of the squamosal. The mesethmoid is not visible dorsally. See Table 8.

Siphonops Wagler

Siphonops Wagler, Isis, von Oken, Leipzig, 1828, p. 742, pl. 10, figs. 1, 2. The type of the genus is *Caecilia annulata* Mikan, by monotypy.

In an article, Isis, von Oken, 1828, "Anszüge aus seinem Systema Amphibiorum" Tab. X., descriptions and comments on several genera are given by Wagler. He includes a single species, *annulatus,* in *Siphonops,* seemingly attributing it to himself, citing Wagler's "Serpentes brasiliens" pl. 26, fig. 1. In his Natürliches System der Amphibien, 1830, p. 198, the single species *Caecilia annulata* is properly attributed to Mikan.

The genus as now understood includes six species: the type *Siphonops annulatus* Mikan, *S. paulensis* Boettger, *S. hardyi* Boulenger, *S. insulanus* Ihering, *S. confusionis* Taylor, and *S. leucoderus* Taylor. One species that has been associated with the genus, *Siphonops brasiliensis,* I regard as belonging to a genus *Luetkenotyphlus* Taylor.

Siphonops has been characterized as lacking secondary folds, being without scales, the tentacle much nearer to the eye than to the nostrils, the eye in a socket that is continuous with the tentacular aperture, and having a very narrow diastema between the squamosal and parietal. The splenial teeth are lacking, and there is no terminal sucking disc. There is a well-defined unsegmented terminal "shield."

Skulls of two species, *Siphonops annulatus* and *S. paulensis* have been available.

Siphonops annulatus (Mikan)

(Figs. 36-38)

Caecilia annulata Mikan, Delectus florae et faunae brasiliensis, Vidabonae, 1820, folio, pl. 11. Type-locality, Sebastianopolis (=Rio de Janeiro), Brasil.

Data here given are principally from the skull of MCZ No. 19407, from "Río Pastazo to Marañon," Ecuador.

This species lacks prefrontals, septomaxillae, and oculars, and has the premaxillae and nasals fused. The mesethmoid is moderately large, completely separating the frontals. The latter are greatly narrowed on their inner margins so that their contact with the mesethmoid is less than one fifth of their length, measured on their outer margins. The parietals, on the other hand, have their greatest length on their inner margins, sometimes more than double the length of their outer margins.

The orbits and the tentacular apertures are continuous with each other, cut between the squamosals and the maxillopalatines. The stapes are present but relatively small and slender. The prevomers are relatively large, extending back a little beyond the internal nares. Following the nares are large diastemata between the basisphenoid and the palatal shelves of the maxillary; the internal nares are almost completely surrounded by the palatine shelves, the prevomers touching them only on their anterior borders for a short distance. The pterygoids are widened, and seemingly fused to the quadrate; ectopterygoids are present.

A second skull, UIM No. 56668, agrees very well with that described. In this it is likewise difficult to interpret the relationship between the pterygoid and quadrate. Anteriorly the pterygoid is attached to the palatine shelf by thin cartilage rather than by overlap.

A third skull, EHT-HMS No. 1848, purporting to be of this species, is from Teresopolis, Guanabara, Brasil. It seems to differ in that if the pterygoid is present, it is seemingly fused solidly with the quadrate. If an ectopterygoid was present, it has been lost. The shape of the stapes is slightly different. See Table 9.

Siphonops paulensis Boettger

(Fig. 39)

Siphonops paulensis Boettger, Katalog der Batrachier Sammlung im Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main, 1892, p. 62. Type-locality, São Paulo, Brasil.

The data here given are taken from the skull of AMNH No. 23433, "Brasil." (Skull partly broken.)

This differs from the preceding species in having the stapes differently shaped. Also in this species the palatine shelves *completely surround* the internal nares. Ectopterygoids are present and each seemingly has one tooth. See Table 9.

Wiedersheim, in his "Anatomie der Gymnophionen" Jena, 1879, pl. 1, figs. 1-12, gives figures of *"S. annulatus."* These however may well be *S. paulensis,* since this species was not recognized until three years later. The external appearance of the two species in preservatives is very similar.

Geotrypetes Peters

Geotrypetes Peters, Sitzb. Ges. Naturf. Freunde, Berlin, 1882, p. 55. The type-species is *Caecilia seraphini* A. Duméril, by monotypy.

Peters (1879) originally placed the type species in the genus *Hypogeophis.*

TABLE 9. Measurements in mm and tooth counts of skulls of *Siphonops*.

Species Number Museum Locality	*annulatus* 19407 MCZ Ecuador	*annulatus* 56668 UIM Limón Cocha, Ecuador	*annulatus* 1848 EHT-HMS Teresopolis, Guanabara, Brasil	*paulensis* 23433 AMNH "Brasil"
Total length of skull	15.4	15.4	13.0	13.7
Greatest width	11.0	11.2	9.4	9.55
Width at orbit	9.1	9.3	7.9	8.0
Length of jaws	14.8	15.1	12.7	12.7
Length of basisphenoid	9.9	10.4	8.3	8.5
Width at "wings"	6.2	6.8	5.2	5.7
Width at otic capsules	6.8	6.4	6.0	6.2
Length of prevomers	4.2	5.2	3.5	4.2
Combined width of prevomers	5.0	5.0	3.9	3.8
Anterior border internal nares to condyle	10.2	10.4	8.55	9.6
Premaxillary teeth	12-11	10-10	8.7	8+-?
Maxillary teeth	7-7	8-7	7-7	11-?
Prevomerine teeth	7-7	8-6	6-6	7-?
Palatine teeth	10-9	10-10	8-8	11-?
Dentary teeth	16-16	15-15	11-11	15-?
Splenial teeth	0-0	0-0	0-0	0-0
Total length of specimen	356	397	?	453

Since 1880, Parker (1936) has described *Geotrypetes angeli* and recognized a new subspecies *G. seraphini occidentalis*. Taylor (1968) described *G. congoensis* and *G. pseudoangeli*.

Geotrypetes seraphini seraphini (A. Duméril)

(Fig. 40)

Caecilia seraphini A. Duméril, Archiv. Mus. Nat. Hist., 1859, vol. 10, p. 222. Type-locality, Gaboon.

Two skulls are at hand, AMNH No. 23466, South Cameroons and MCZ No. 3424, Metet, Cameroons. The data here presented are from the second.

This skull is quite remarkable in having teeth on the ectopterygoid, which lies below the pterygoid. Dorsally the mesethmoid separates the frontals for nearly half their length. Diastemata are present between the parietals and squamosals which run forward into the orbit. The tentacular apertures emerge at the orbits and, as deep, wide-open grooves, run forward to a point on the nasomaxillae. On the ventral surface the prevomers do not reach as far back as the middle of the internal nares. The prevomers each have a large fenestra and a median forward projection anterior to the prevomerine teeth. They are separated for most of the length behind the teeth by a spine of the basisphenoid. The maxillopalatines *completely sur-*

round the internal nares, behind which are enormous diastemata between the basisphenoid and palatine shelves, and the pterygoids. See Table 10.

The "wings" of the basisphenoid are greatly narrowed as compared with skulls of other genera. The skulls of *Geotrypetes* as far as known, differ from most of the other genera of the subfamily Dermophinae of the Caeciliidae in that they have ectopterygoid teeth and have the diastemata between the squamosals and parietals penetrating the orbital rim. The skulls are seemingly more fragile than is usual in other genera of the family.

Geotrypetes seraphini occidentalis Parker

(Fig. 41)

Geotrypetes seraphini occidentalis Parker, Zool. Meded. Rijks. Mus. Nat. Hist., Leiden, 1936, pp. 99-100. Type-locality, French Guinea and the Gold Coast Region (Ghana).

Data here given are taken from the skull of EHT-HMS No. 4653, Tafo, Ghana.

Dorsally the mesethmoid separates the frontals, runs forward separating the nasopremaxillae for a distance, and then appears again at their anterior parts; posteriorly the anterior prongs of the parietals are likewise separated by the mesethmoid. The parietals narrow mesially with their posterior parts declivous. Broad diastemata are present between the squamosals and parietals; also, the suture between the anterior part of the squamosal and parietal and the squamosal and frontal runs forward, breaking the continuity of the large orbit of the eye. The orbit is continuous with the proximal part of the tentacular groove. The tentacular groove is open for a short distance, then is covered over by bone of the maxillopalatine, but later emerges from under the anterior part of this same bone, the groove continuing forward to a point below but near the back edge of the nostril. The orbital opening is large and somewhat pear-shaped. Two processes of the prevomer run forward anterior to the prevomerine teeth. Posteriorly the prevomers are separated by the short spine of the basisphenoid for a distance, with their posterior ends not reaching to the level of the middle of the internal nares. The nares are *completely surrounded* by the maxillopalatine. There are two very large openings posterior to the nares. The ectopterygoids bear teeth (not visible in the Figure); the pterygoid touches the palatine shelf; the wings of the basisphenoid are much narrowed. See Table 10.

Herpele Peters

Herpele Peters, Monatsb. Akad. Wiss. Berlin, 1879, p. 939. Type of genus, *Caecilia squalostoma* Stutchbury, by monotypy.

Peters defined this genus on the basis of the following characters: eye under the skull bones; tentacular aperture circular, behind and below nostril; similar to *Hypogeophis rostratus*. Scales in folds; two tooth rows in lower jaw.

Herpele squalostoma (Stutchbury)

(Fig. 42)

Caecilia squalostoma Stutchbury, Trans. Linnean Soc. London (1), vol. 17, 1837, p. 362. Type-locality, Gaboon.

Data here recorded are from a skull of EHT-HMS No. 3412 from Metet, Cameroons, Africa.

The mesethmoid appears minutely at the anterior and posterior ends of the common suture between the frontals; in neither case is the visible part more than 0.5 mm long. The eye is under the squamosal bone. This bone is rather elongate but not as long as the maxillopalatine. The tentacular aperture is at anterior end of the maxillopalatine, with the groove continued slightly along the nasopremaxilla, the apertures barely visible from the ventral face of skull. The prevomers are short and separated by the spine of the basisphenoid for less than half their length, their posterior extentions being somewhat widened and lying below the basisphenoid instead of above it as in *Oscaecilia,* their forward extensions reaching anterior to the prevomerine teeth. There is a diastema between the basisphenoid and the palatine shelves, the small forward-extending part of the pterygoid is above the palatine shelf rather than on its inner edge. Small ectopterygoids are present, touching the pterygoid. The otic capsules are somewhat inflated. See Table 10.

Uraeotyphlus Peters

Uraeotyphlus Peters, Monatsb. Akad. Wiss. Berlin, 1879, p. 933. Type-species, *Caecilia oxyura* Duméril and Bibron, by subsequent designation.

Peters (1879) assigned two species to the genus, the type and *Caecilia malabarica* Beddome. Boulenger (1882) later described *Uraeotyphlus africans* (now transferred to *Geotrypetes seraphini seraphini*). Annandale (1913) described *Uraeotyphlus menoni* and Seshachar (1939) described *U. narayani.*

Now four species are recognized in the genus. All are Indian in distribution. Peters reports *oxyurus* from the Seychelles Islands but this doubtless is in error.

Uraeotyphlus oxyurus (Duméril and Bibron)

(Fig. 43)

Coecilia oxyurus Duméril and Bibron, Erpétologie générale, 1841, vol. 8, p. 280. Type-locality, Malabar, India.

Data here recorded are from the skull of MCZ 9484, Taliparabamba, Travancore, India.

The mesethmoid does not appear on the dorsal skull surface. The prefrontals and septomaxillae are not present and the premaxillae and nasals are fused, forming the large nasopremaxillae. The eye is in an orbit that is continuous with the deep open groove of the tentacle. This extends forward to a point below the back edge of the nostril. The orbits are bordered for more

TABLE 10. Measurements in mm and tooth counts of skulls of *Geotrypetes, Herpele, Uraeotyphlus* and *Schistometopum.*

Species Number Museum Locality	*G. s. seraphini* 3424 MCZ Metet, Cameroons	*G. s. occidentalis* 4653 EHT-HMS Tafo, Ghana	*H. squalostoma* 3412* EHT-HMS Metet, Cameroons	*U. oxyurus* 9484 MCZ Taliparamba, Travancore	*S. gregorii* 20117 MCZ Lake Peccatoni, Kenya	*S. gregorii* 20146 MCZ Lake Peccatoni, Kenya
Total length of skull	9.0	11.3	10.7	7.8	10.4	10.5
Greatest width	6.0	7.7	6.45	4.3	6.3	6.7
Length of jaw	8.0	....	.	....	9.5	9.5
Length of basisphenoid	6.8	8.3	7.2	5.0	7.1	7.3
Width at wings	3.7	5.2	4.0	2.7	3.8	4.1
Width at otic capsules	3.9	6.4	4.4	3.35	4.5	4.65
Length of prevomers	2.1	3.0	2.3	2.4	2.2	2.3
Combined width of prevomers	2.0	2.8	3.1	. .	2.9	3.1
From anterior border of internal nares to condyle	6.0	7.7	7.2	5.0	6.6	7.0
Premaxillary teeth	5-4	5-4	4-5	5-4	6-7	7-7
Maxillary teeth	12-12	12-11	12-11	11-13	8-8	10-9
Prevomerine teeth	5-4	4-5	6-7	7-7	5-5	6-6
Palatine teeth	12-12	10-10	11-10	10-11	11-10	10-9
Dentary teeth	18-19	16-16	12-11	12-12	11-12	15-14
Splenial teeth	10-10	17-16	3-3	8-8	1-1(?)	1-1
Ectopterygoid teeth	5-5	5-5	0-0	0-0	0-0	0-0
Total length of specimen	?	354	357	215	336	356

than half of their circumference by free, narrow, curved ocular bones (postfrontals), while below they are bordered by the maxillopalatines. The stapes are present, touching the quadrates. The prevomers extend forward a little beyond the prevomerine teeth, while posteriorly they reach to the posterior level of the the internal nares, the spine of the basisphenoid separating them for about one fifth of their total length. They border the inner sides of the internal nares but for the greater part of their circumference the nares are bordered by the palatine shelves of the maxillae. See Table 10.

The skull is defective, broken, and parts missing, so that certain characters cannot be examined and recorded.

Schistometopum Parker

Schistometopum Parker, Ann. Mag. Nat. Hist., ser. 11, vol. 7, p. 17, fig. 4. Type-species, *Dermophis gregorii* Boulenger, by designation.

Two species were originally assigned to the genus, *S. gregorii,* and *S. thomensis* (Bocage). Peters described *Siphonops brevirostris* in 1874 which has been regarded a synonym of *S. thomensis* by certain authors. Taylor (1964) described *Schistometopum ephele.*

Schistometopum gregorii (Boulenger)

(Figs. 44-45)

Dermophis gregorii Boulenger, Proc. Zool. Soc. London, 1894, p. 646, pl. 40, fig. 4. Type-locality, Ngatana, Tana River, Kenya.

Data recorded are from the skull of MCZ No. 20117, Lake Peccatoni, Kenya.

This species has been redescribed by Nieden (1912) as *Boulengerula denhardti* from the Tana Region, Kenya and by Boettger (1913) as *Bdellophis unicolor in* Voeltzkow from Lake Peccatoni, Wituland, Kenya.

The slender mesethmoid separates the frontals and pushes in slightly between the nasopremaxillae. The eye orbits are cut between the squamosal and the maxillopalatine, but lie chiefly in the former. The tentacular apertures appear near the anterior end of the maxillopalatines, which are definitely shorter than the squamosals. The stapes are much constricted behind the point of contact with the quadrates.

The prevomers are very short, projecting forward beyond the prevomerine teeth for a short distance, but not reaching back as far as the middle of the internal nares. The diastemata between the basisphenoid and palatal shelves are small. Seemingly small ectopterygoids are present (broken in this specimen).

A second skull, MCZ 20146, agrees in all essential details with the preceding. See Table 10.

Hypogeophis Peters

Hypogeophis Peters, Monatsb. Akad. Wiss. Berlin, 1879, p. 936. Type-species *Caecilia rostrata* Cuvier.

Peters (1879) considered two species as belonging to the genus, the type, and *Caecilia seraphini* A. Duméril. In 1880 he proposed *Geotrypetes* as a new genus for the second species.

Parker (1941, 1958), who reviewed the species of *Hypogeophis,* concluded that there was a single species *H. rostratus,* with three subspecies: *H. r. rostratus, H. r. guentheri* Boulenger, and *H. r. praslini* Parker. All are confined to the Seychelles Islands in the Indian Ocean, but each has its own range, on different islands. Taylor (1969a) has added a fourth subspecies, *H. r. lionneti.*

Hypogeophis rostratus rostratus (Cuvier)

(Fig. 46)

Caecilia rostrata Cuvier, Règne Animal, 2nd ed. 1829, vol. 2, p. 100. Type-locality, Mahé, Seychelles (most probably).

Data here recorded are taken from the skull, MCZ No. 48935.

The prefrontals, septomaxillae, and oculars are absent or fused to surrounding bones and the premaxillae and nasals are fused to form the nasopremaxillae. The stapes are present. The mesethmoid does not appear on the dorsal surface of the skull. The basisphenoid is fused with the various occipitals and otic elements to form a compound bone (as in all gymnophiones).

The eye socket is cut in the squamosal. The tentacular apertures are separate from the orbits, opening far forward at the end of the maxillopalatines, the grooves continuing forward along the nasopremaxillae, the openings partially visible in a ventral view. No diastemata are present between the squamosals and parietals. The internal nares are largely surrounded by the maxillopalatines, but the prevomers border them on the anterior inner edge.

There are very small diastemata behind the internal nares between the basisphenoid and palatal shelves of the maxillopalatines. The basisphenoid separates only the posterior tips of the prevomers and is strongly constricted in front of the otic capsules. The pterygoids seemingly are fused to the quadrate, and relatively narrow. A small ectopterygoid is present. There appears to be a small element separated from the palatine portion of the maxillopalatine which, if it touches the pterygoid, does so below the lateral wings of the basisphenoid. The snout projects considerably beyond the premaxillary teeth. See Table 11.

Grandisonia Taylor

Grandisonia Taylor, Caecilians of the World, 1968, p. 749, fig. 409. Type of genus, *Hypogeophis alternans* Stejneger.

Taylor referred three species to the genus. These were *Hypogeophis alternans* Stejneger, *Dermophis sechellensis* Boulenger, and *Dermophis larvata* Ahl. In addition, two other species were referred with some doubt, *Hypogeophis brevis* Boulenger and a new species *Grandisonia diminutiva*

Taylor, since neither the anatomy nor the life histories of these diminutive species are known. They are the smallest species of the Gymnophiona.

Grandisonia alternans (Stejneger)

(Fig. 47)

Hypogeophis alternans Stejneger, Proc. U.S. Nat. Mus. Washington, 1893, vol. 16, p. 739; type-locality, Mahé, Seychelles Islands.

Skull data here recorded are of EHT-HMS No. 4647, from Mahé, Seychelles.

The skull has the typical reduced number of bones of the family Caeciliidae. The mesethmoid does not appear on the dorsal surface of the skull. There are no distinct diastemata between the squamosals and the parietals; the suture, however, is cartilage covered and when this is removed there is a slight break between them. The rims of the orbits, between the squamosals and the maxillopalatines, are continuous with the tentacular apertures and the tentacular grooves which run forward to the anterior end of the maxillopalatines. The stapes are prominent.

On the ventral surface of the skull the basisphenoid is strongly constricted between the otic capsules and the "wings," and tapers anteriorly to a spine, which, running forward, separates the prevomers for more than half their length. The prevomers are wide, anteriorly they scarcely extend beyond the prevomerine teeth; posteriorly they do not reach the middle of the internal nares, but border the nares for a short distance. An ectopterygoid is present; the pterygoid is seemingly fused to the quadrate. There are small diastemata between the basisphenoid and the palatine shelves of the maxillopalatines. The separation between the internal nares is greater than usual because the part of the basisphenoid extending between the prevomers is widened, thus greatly narrowing the prevomers posteriorly. See Table 11.

Grandisonia sechellensis (Boulenger)

(Fig. 48)

Dermophis sechellensis Boulenger, Trans. Linnaean Soc. London; Zool., 1911, vol. 14, p. 376, fig. 3. Type-locality, Mahé, Seychelles.

Hypogeophis sechellensis Parker, Am. Mag. Nat. Hist. (1941), ser. 11, vol. 7, p. 16, fig. 2.

The data here given are from a damaged skull, AMNH 23673, "Seychelles Islands," with no specific locality.

Mr. Boulenger and Dr. Parker studied the caecilians of the Seychelles. Boulenger (1909) referred some specimens of this species to his *Cryptopsophis multiplicata*, and two years later described them as a new species, *Dermophis sechellensis*. Parker first regarded this species as a *Dermophis* (1941). Ahl (1926) had described it as *Dermophis flaviventer*. Parker later (1958) referred it to *Hypogeophis sechellensis* and still later seemingly regarded it as a member of the genus *Praslinia* Boulenger. Taylor (1968) placed it in his genus *Grandisonia*.

This skull differs very little from Parker's figure *(loc. cit.)*, the nasopremaxillary is proportionally longer with no trace of a mesethmoid dorsally. (A slight exposure of this element shows in Parker's figure.) The outer edges of the frontals are longer, and the parietals are less constricted anterior to their middle.

On the ventral surface of the skull the prevomers are short, reaching to the anterior part of the internal nares, and are separated for about half their length by the spine of the basisphenoid. There is a strong constriction of the basisphenoid just anterior to the otic capsules. The eye orbit is cut chiefly in the squamosal but its border is continuous with the tentacular aperture. A pterygoid process and an ectopterygoid are present. See Table 11.

Idiocranium Parker

Idiocranium Parker, Proc. Zool. Soc. London, 1936, pp. 160-163. Type of genus, *Idiocranium russeli.*

This genus has certain characters which are unique in the Gymnophiona. These were recognized by Dr. Parker who has given an excellent description of this diminutive creature.

Idiocranium russeli Parker

(Fig. 49)

Idiocranium russeli Parker, Proc. Zool. Soc. London, 1936, pp. 160-163, figs. 6, 8. Type-locality, Makumunu, Asumbo, Mamfe Division, Cameroons (now included in Nigeria?).

The data recorded here are taken from EHT-HMS No. 4687. Paratype.

The large dorsal nasopremaxillae are separated their entire length by a large, somewhat triangular mesethmoid which runs forward, terminating in a point. Following this on the dorsal surface of the skull is a pair of small subquadrangular frontals which are separated from the maxillopalatines by the contact of the nasopremaxillary with the squamosal, and having an area less than one third that of the parietals. The orbits of the eyes are between the elongate squamosals and the maxillopalatines. The larger tentacular apertures emerge from the anterior ends of the maxillopalatines and the tentacular groove continues forward some distance beyond the opening, along the side of the nasomaxillae. The stapes is well defined, the "neck" joining the quadrate being very short. The otic capsule is distinctly inflated.

The internal nares are surrounded by the maxillopalatines and the prevomers, the latter bones bordering their inner edges for a short distance, then extending back to the posterior level of the internal nares; there are no diastemata between the basisphenoid and the palatine shelves of the maxillae. The pterygoid reaches forward one third of the way to the internal nares. No ectopterygoid is present. See Table 11.

The greatly enlarged mesethmoid, the separation of the nasopremaxillae, the reduction of the size of the prefrontals and the separation of the frontals

TABLE 11. Measurements in mm and tooth counts of skulls of *Hypogeophis*, *Grandisonia*, *Idiocranium* and *Boulengerula*.

Species	*H. r. rostratus*	*G. alternans*	*G. sechellensis*	*I. russeli*	*B. boulengeri*
Number	48935	4647	23673	4687	12309
Museum	MCZ	EHT-HMS	AMNH	EHT-HMS	MCZ
Locality	St. Anne Island	Mahé	"Seychelles"	Makumunu	Amani, Usambara Mts., Tanganyika
Total length of skull	8.6	11.1	5.15	4.5	4.7
Greatest width	5	7	2.8	2.2	2.3
Width at orbits	4	....	2.45	1.7	3.4
Length of jaw	7.4	10	....	....	4.3
Length basisphenoid (ventral)	5.3	8	4.2	3.35	2.65
Width at "wings," greatest	3.3	4.25	1.8	1.7	1.4
Width at otic capsules	3.7	4.8	2.25	2.05	1.75
Length of prevomers	2.2	2.6	1.2	1.0	0.9
Greatest combined width of prevomers	1.75	2.7	1.0	0.9	0.9
Length anterior nares to occipital condyle	5.2	5.5	3.5	3.2	4.5
Premaxillary teeth	6-6	9-9	7-7	6-6	4-5
Maxillary teeth	18-18	15-14	12-13	13-14	5-6
Prevomerine teeth	9-8	8-8	8-7	6-6	4-4
Palatine teeth	17-17	16-15	13-13	11-12	8-8
Dentary teeth	14-13	20-20	12-?	11-12	8-8
Splenial teeth	3-3	6-5	7-?	2-2	0-0
Total length of specimen in preservation	254	?	?	?	178

from the maxillopalatine easily distinguish this genus from all other Gymnophiona.

Boulengerula Tornier

Boulengerula Tornier, Kriechthiere Deutsch-Ost-Afrikas, Beiträge zur Systematik und Descendenzlehre. Berlin, 1897, p. 164 (type of the genus, *B. boulengeri* from Usambara Mts., Tanganyika [Tanzania] Africa).

Generic characters indicated by Tornier are: parietal and squamosal forming a suture without diastema; no splenial teeth present; eyes roofed over by bone; no scales present; tentacle conical and extrusible, equally distant from nostril and symphysis of jaws. Only the type species is known.

Boulengerula boulengeri Tornier

(Fig. 50)

Boulengerula boulengeri Tornier, Kriechthiere Deutsch-Ost-Afrikas. Beiträge zur Systematik und Descendenzlehre. Berlin, 1897, p. 164. Type-locality Usambara Mts., Tanganyika (Tanzania), Africa.

Data are from a defective skull, MCZ No. 12309, Amani, Usambara Mts., Tanganyika (Tanzania), Africa.

The skull agrees with family characters in reduction of the number of dorsal skull bones; the mesethmoid appears narrowly on the median dorsal line, completely separating the prefrontals and forming a very slight wedge between the posterior ends of the nasopremaxillae, and a larger wedge between the anterior ends of the parietals. The median length of the frontals is about half the median length of the parietals.

There is no eye socket; the eye, if present, is bone covered. The tentacular aperture is cut in the maxillopalatine, its groove not extending beyond these. The parietals and squamosals form sutures without diastemata, the parietals widening very slightly behind the posterior level of the squamosals. The snout projects beyond the mouth. The basisphenoid is relatively very wide anteriorly at the point of contact with the prevomers, except for a spine from the basisphenoid that separates the greatly narrowed prevomers for half of their length. The prevomers reach posteriorly behind the posterior level of the internal nares.

A short break occurs in the continuity of the prevomeropalatine tooth series. The pterygoids are present and fused to the quadrate. The otic capsules are obviously inflated. See Table 11.

Afrocaecilia Taylor

Afrocaecilia Taylor, Caecilians of the World, 1968, p. 321. Type of the genus, *Boulengerula taitanus* Loveridge.

Afrocaecilia is characterized as follows: eye under bone; tongue free laterally and anteriorly; no scales; no secondaries; splenial teeth present; tentacle small, distanct from nostril; no tail; an unsegmented terminal "shield."

Taylor referred three species to the genus: the type, *Boulengerula taitanus*, *B. uluguruensis* and *B. changamwensis*. All are small species, east African in distribution. The members of the genus may readily be differentiated from *Boulengerula* by the presence of splenial teeth.

Afrocaecilia uluguruensis (Barbour and Loveridge)

(Fig. 51)

Barbourula uluguruensis Barbour and Loveridge, Mem. Mus. Comp. Zool., Harvard College, vol. 50, 1928, pp. 183-184. Type-locality, Vituri (2000 ft. elev.), Uluguru Mountains, Northeastern Tanganyika (Tanzania).

One skull from a topotypic paratype has been available for study, EHT-HMS No. 4649. The characteristics are as follows:

The eye if present, is concealed under the squamosal bone. The tentacular aperture is at or near the anterior end of the maxillopalatine, which is relatively small. The nasopremaxilla is relatively large, the mesethmoid not being visible on the dorsal surface of skull. The frontals are quadrangular, their common suture about equaling half of the common parietal suture length.

The prevomers are separated by the spine of the basisphenoid for more than two thirds of their length. Very narrow diastemata posterior to the internal nares lie between the maxillopalatine shelf and the basisphenoid. The basisphenoid is widened where it first meets the prevomers. The pterygoid appears to be fused with the quadrate. The lateral sutures of the maxillopalatine are difficult to follow. See Table 12.

Afrocaecilia taitana (Loveridge)

(Fig. 52)

Boulengerula taitanus Loveridge, Bull. Mus. Comp. Zool., Harvard College, vol. 79, 1935, p. 16. Type-locality, Mt. Mbololo (4800 ft. elev.), Teila Hills, Kenya.

Data here are recorded from the skull of MCZ No. 20021, topotype.

The characters differing from *A. uluguruensis* are: the skull is longer and perhaps slenderer, the prevomers may reach back only to the posterior level of the internal nares (not distinctly farther as in *A. uluguruensis*), and an ectopterygoid is present (seemingly absent in the two other species). It has been injured during the lifetime of the animal, as one of the bones on the head has been broken and partially mended. See Table 12.

Afrocaecilia changamwensis (Loveridge)

(Fig. 53)

Boulengerula changamwensis Loveridge, Bull. Mus. Comp. Zool., Harvard College, 1932, vol. 72, p. 381. Type-locality, Changamwe (192 ft. elev.) near Mombasa, Kenya, Africa.

Data are from the skull of a topotypic paratype, EHT-HMS No. 4651.

The differences of this skull from the above two are small. The prevomers are somewhat differently shaped as is the anterior spine of the basi-

TABLE 12. Measurements in mm and tooth counts of skulls of *Afrocaecilia*.

Species Number Museum Locality	*uluguruensis* 4649 EHT-HMS Uluguru Mts.	*taitana* 20021 MCZ Teita Hills, Kenya	*changamwensis* 4651 EHT-HMS Changamwe, Kenya
Total length of skull	5.8	7.3	5.7
Greatest width	3.2	3.6	3.25
Length of lower jaw	5.2	6.3	5.1
Length of basisphenoid	4.4	3.5	4.2
Width at otic capsules	2.0	2.6	2.05
Width at "wings"	1.35	2.35	1.8
Length of prevomers	1.4	1.7	1.7
Combined width, greatest	1.5	1.85	1.5
Anterior border of internal nares to end of skull	3.55	4.7	3.7
Premaxillary teeth	6-8	?-?	6-7
Maxillary teeth	?-8	12-11	8-?
Prevomerine teeth	5-4	4-5	5-4
Palatine teeth	6-7	9-8	?-10
Dentary teeth	10-10	12-12	10-10
Splenial teeth	3-2	1-1	2-2
Total length of specimen	232	?	234

sphenoid. The fused? pterygoid is present but I am not wholly certain that there is an ectopterygoid. The squamosal is elongate as in the other two skulls. See Table 12.

Gegeneophis Peters

Gegenes Günther, Proc. Zool. Soc. London, 1875, p. 577, type of genus, *Epicrium carnosum* Beddome (preoccupied by Hubner, 1816, for a genus of Lepidoptera).

Gegeneophis Peters, Monatsb. Akad. Wiss. Berlin, 1879, p. 932 (type of genus, *Epicrium carnosum* Beddome).

Gegenophis Boulenger (error or emendation), Catalogue of the Batrachia Gradientia *s.* Caudata and Batrachia Apoda in the Collection of the British Museum, 2nd Ed. 1882, p. 101.

This genus is, so far as known, confined to India. It comprises three species, one of which, *G. fulleri*, may be doubtfully associated. The other two, *G. ramaswamii* and *G. carnosus*, seemingly belong to the same genus.

The type species, *G. carnosus*, is small, and none has been available for an examination of the skull.

The combination of external characters that serve to define the genus are: eye without orbit, solidly covered by bone; splenial teeth present; no diastema between prevomerine and palatine teeth; tentacle small, behind and below nostril; secondary folds present posteriorly; scales are present, two to four rows posteriorly; tongue with two narial plugs, vent transverse.

Gegeneophis ramaswamii Taylor

(Figs. 54, 55)

Gegeneophis ramaswamii Taylor, Senck. Biol., Frankfurt am Main, 1964, Bd. 45, Heft 3/5,

TABLE 13. Measurements in mm and tooth counts of skulls of *Gegeneophis ramaswamii* (topotypic paratypes).

Number	29452	29454	29456
Museum	MCZ	MCZ	MCZ
Locality	Kerala, India	Kerala, India	Kerala, India
Total length of skull	10.0	9.05	8.5
Greatest width	6.0	4.95	5.9
Length of lower jaw	10.0	....	8.3
Length of basisphenoid	6.5	6.0	5.7
Width (at wings)	3.2	2.75	2.85
Width posterior to constriction	4.3	3.4	3.55
Length of prevomers	2.6	2.0	2.00
Combined width of prevomers (greatest)	3.0	2.35	2.3
Anterior border of choana to condyle	6.7	6.0	5.8
Premaxillary teeth	4-5	4-6	5-5
Maxillary teeth	14-15	11-10	10-11
Prevomers teeth	5-5	5-4	5-5
Palatine teeth	12-13	10-12	12-11
Dentary teeth	13-13	....	13-13
Splenial teeth	3-3	....	3-3
Total length of specimen	305	263	242

Dec. 1, 1964, pp. 227-231, text figs. 1, 2 (type-locality Tenmalai Forest, Kerala [state], southern India); Caecilians of the World, Lawrence, Kansas, 1968, pp. 739-746, figs. 402-406.

Data recorded here are from the skull of MCZ No. 29452.

The prefrontals, septomaxillae, and oculars do not appear; the premaxillae and nasals are united. The mesethmoid is not visible dorsally. The posterior part of the skull is declivous, rather abruptly so from the parietal border. The stapes are relatively very large. There is no eye socket. The internal nares are almost surrounded by the maxillopalatines but are bordered for a short distance on their inner side by the prevomer. A small diastema is present between the basisphenoid and pterygoid following the nares.

Two other skulls available do not differ in essential details. See Table 13.

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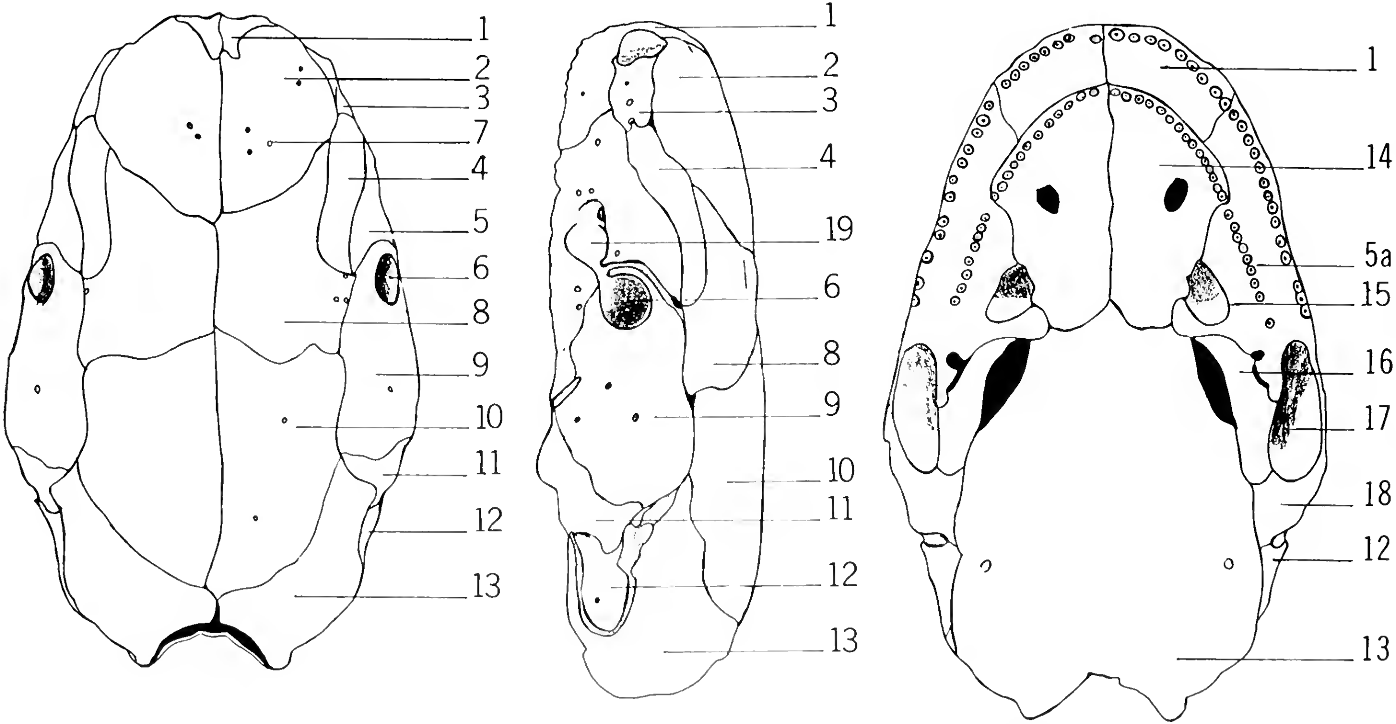

FIG. 1. Generalized diagram of a Caecilian skull. Dorsal, lateral, and ventral views of the skull of *Caudacaecilia weberi* Taylor. 1, premaxilla; 2, nasal; 3, septomaxilla; 4, prefrontal; 5, maxilla; 5a, palatine shelf of maxilla; 6, orbit of eye; 7, fenestra for nerves or blood vessels; 8, frontal; 9, squamosal; 10, parietal; 11, quadrate; 12, stapes; 13, basisphenoid (compound); 14, prevomer; 15, internal naris (choana); 16, pterygoid; 17, fenestra for jaw muscles; 18, quadrate; 19, tentacular groove.

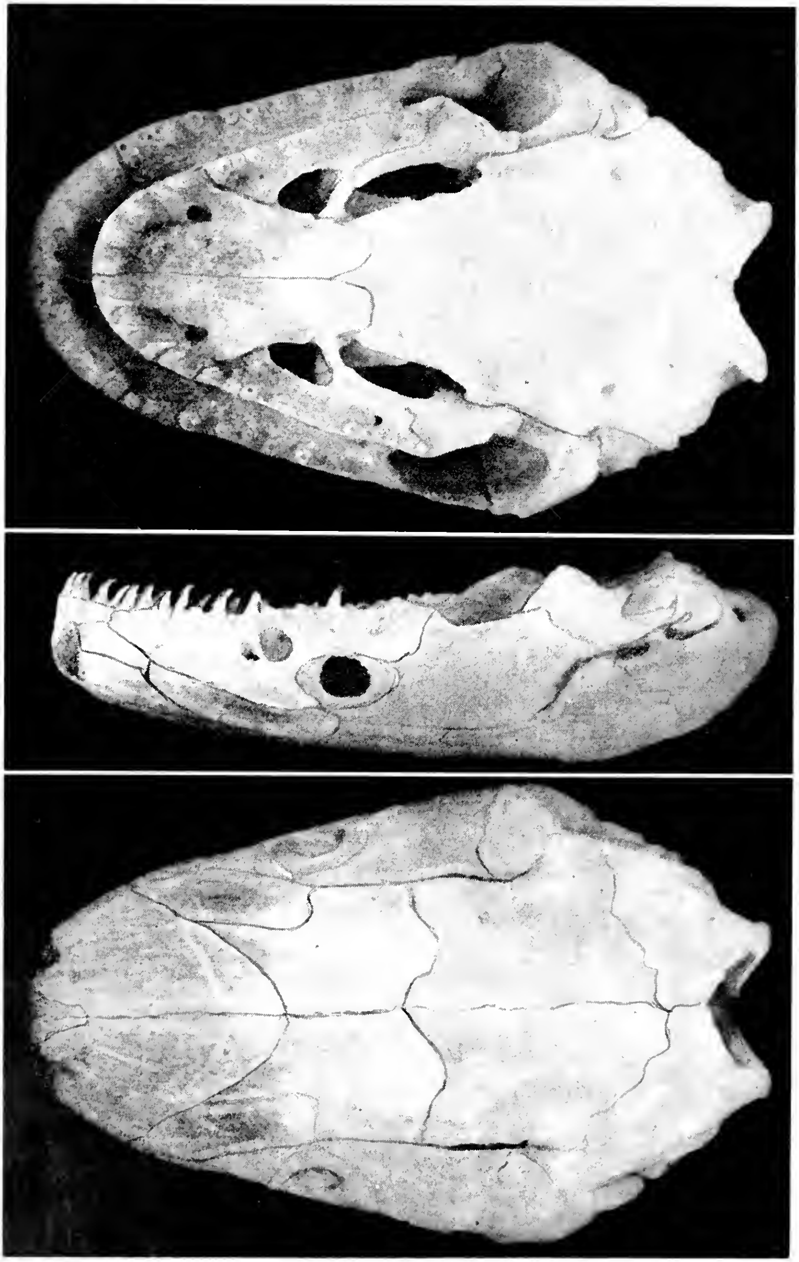

FIG. 2. *Ichthyophis glutinosus* (Linnaeus). KUMNH No. 31291, Numunukula, Tonacombe Estates, Uva Hills, Uva Province, Ceylon. Total length of specimen, 320 mm; length of skull, 13.0 mm; width of skull, 8.0 mm. (Note: ventral portion of squamosal broken, exposing the pterygoid laterally.)

FIG. 3. *Ichthyophis beddomei* Peters. EHT-HMS Coll. No. 3186, Kotegehar, Mysore, India. Total length of specimen, 258 mm; length of skull, 11.0 mm; width of skull, 7.0 mm. (Small break on palatine shelf.)

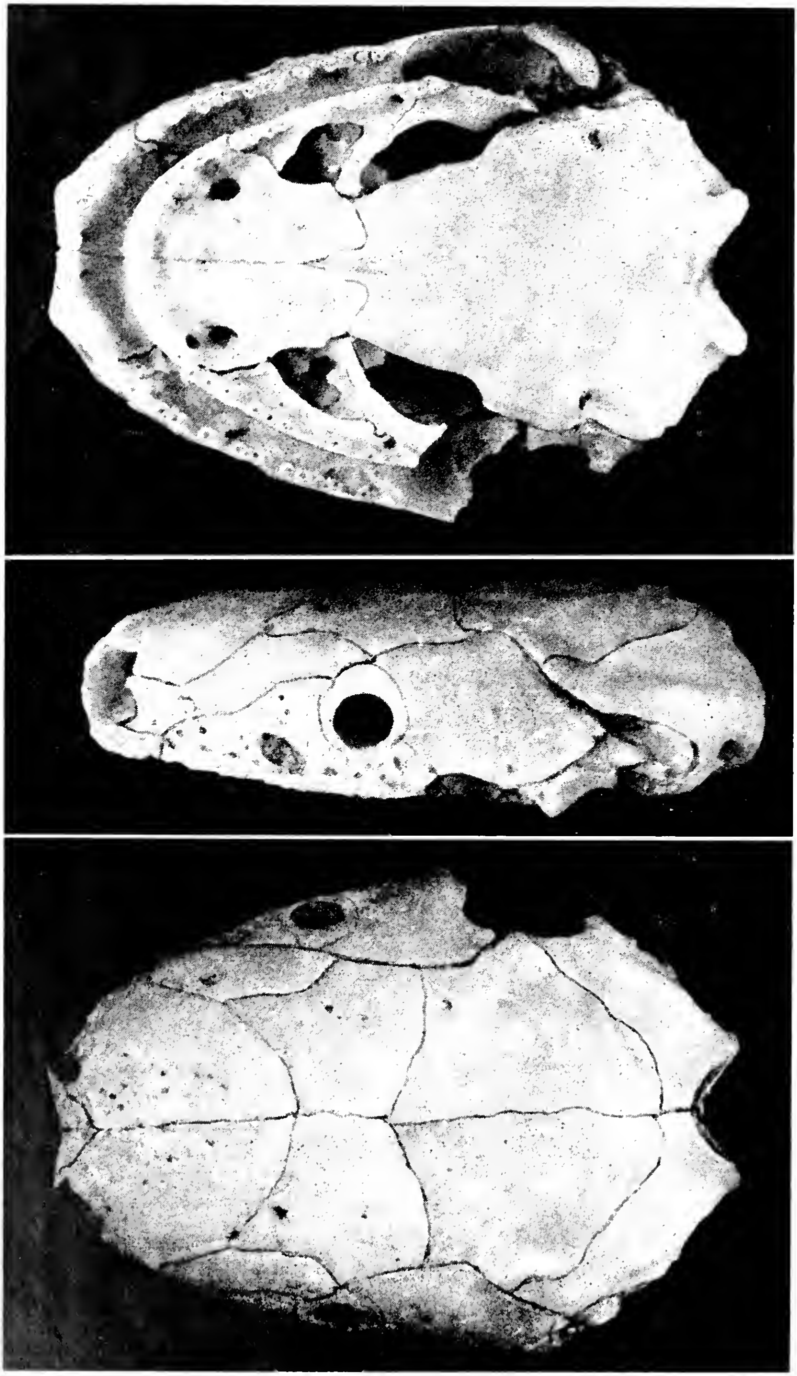

Fig. 4. *Ichthyophis singaporensis* Taylor. BMNH No. RR, 1959.1.2.43. Type. Singapore Island. Total length of specimen, 243 mm; length of skull, 10.4 mm; width of skull, 7.0 mm. (Side of skull broken.)

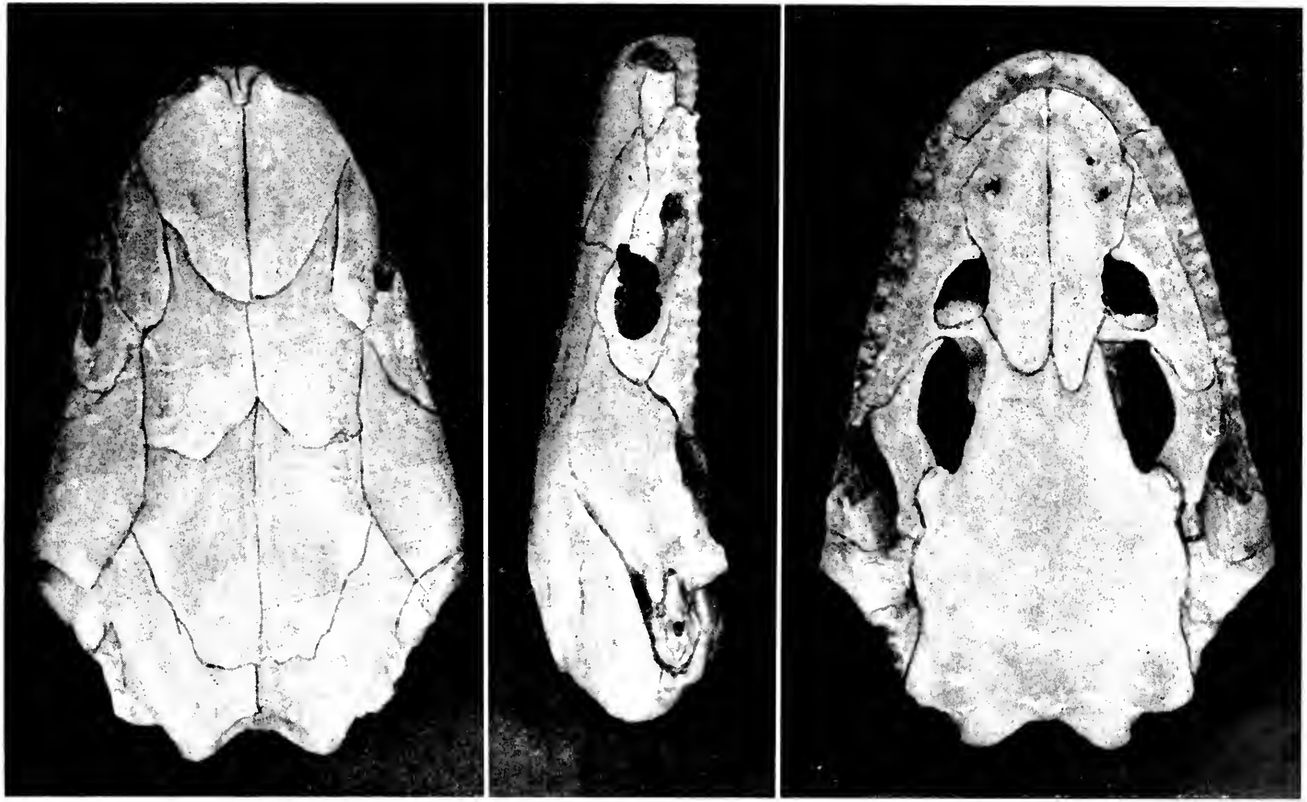

FIG. 5. *Ichthyophis kohtaoensis* Taylor. EHT-HMS Coll. No. 3935. About 10 miles N. of Chiang Dao, Northern Chiang Mai Province, Northern Thailand. Total length of specimen, 309 mm; length of skull, 11.7 m; width of skull, 6.8 mm. (Orbit rim broken, when photographed.)

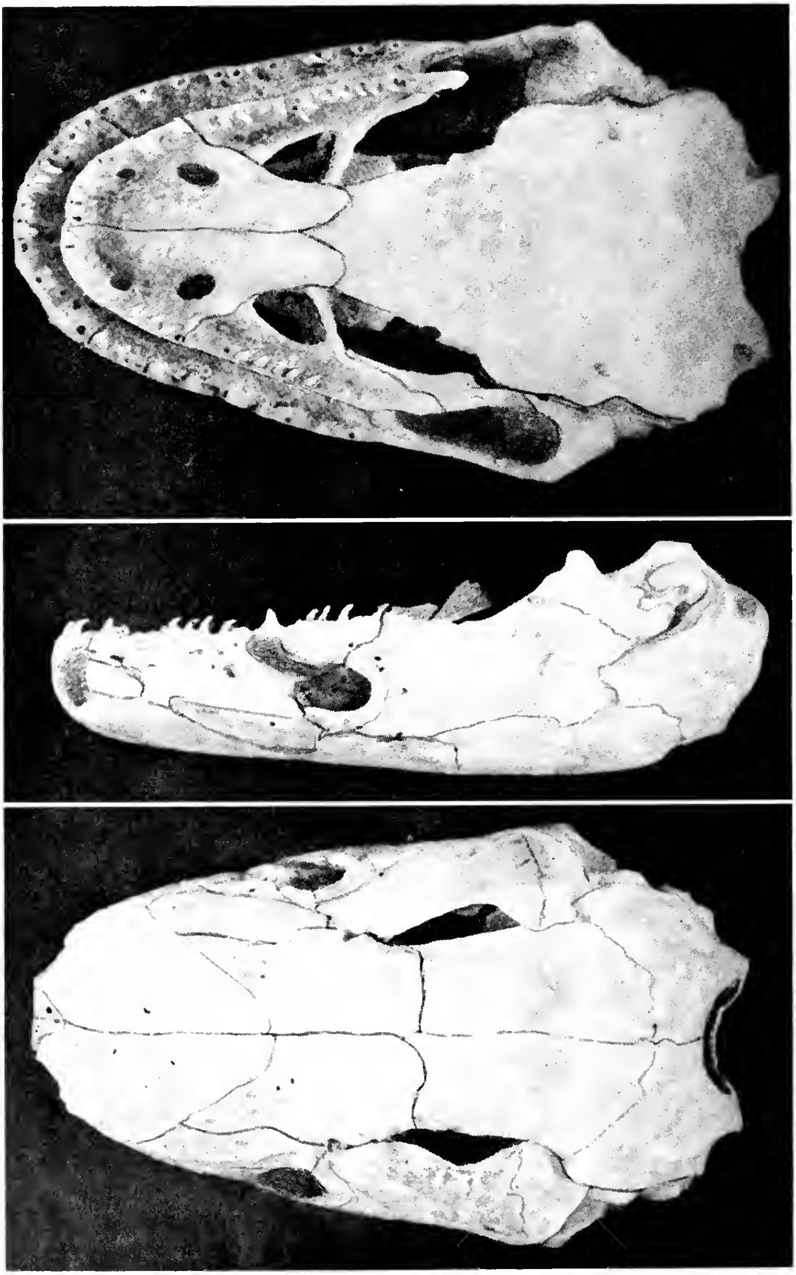

FIG. 6. *Ichthyophis kohtaoensis* Taylor. EHT-HMS Coll. No. 1838, Dansai Prov., Thailand. Total length of specimen, 333 mm; length of skull, 14.0 mm; width of skull, 9.0 mm. (Portion of orbit rim broken; left pterygoid missing.)

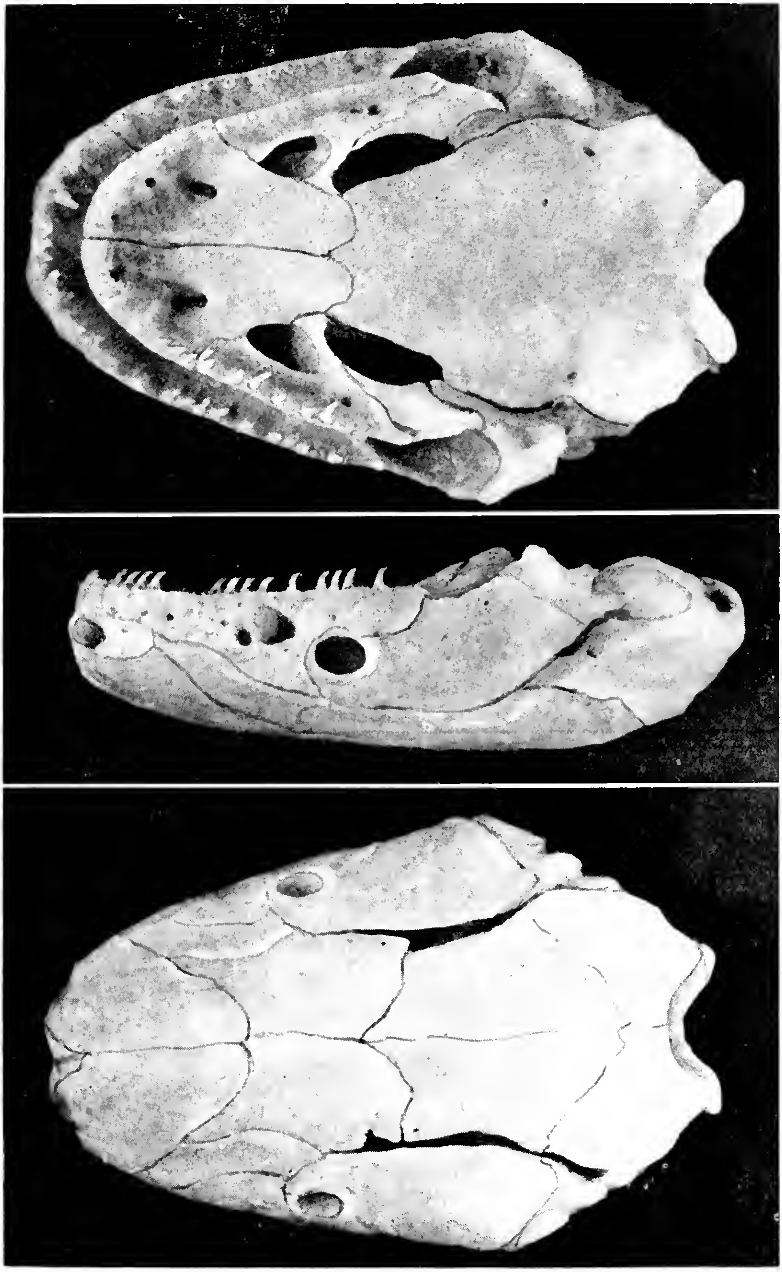

FIG. 7. *Ichthyophis mindanaoensis* Taylor. DSBM No. 20926. Bank of Dapitan River, 11 km. SE Buena Suerte, Misamis, P.I., elev. ca. 3700 ft. Total length of specimen, 259 mm; length of skull, 11.5 mm; width of skull, 7.4 mm.

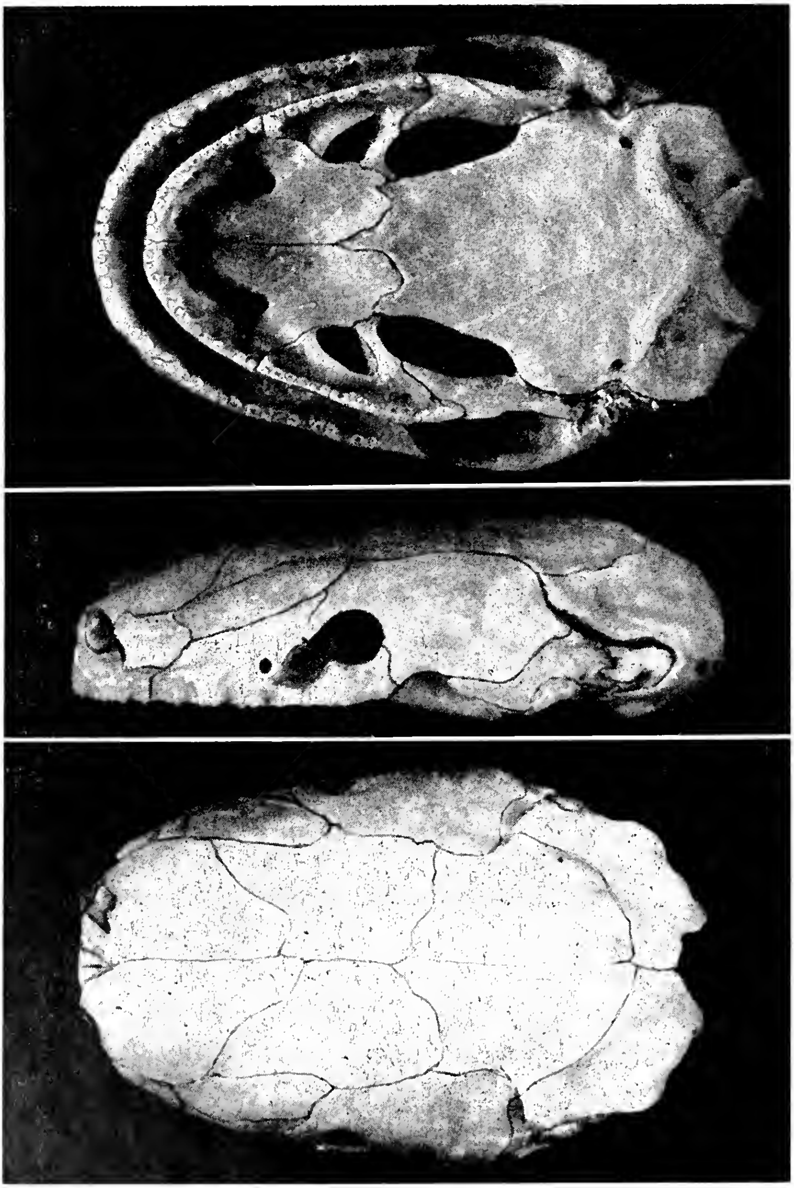

FIG. 8. *Caudacaecilia nigroflava* (Taylor). EHT-HMS Coll. No. 1734. Bukit Lagong Forest Reserve, Selangor, Malaya (near Kuala Lumpur). Total length of specimen, 385 mm; length of skull, 12.0 mm; width of skull, 8.0 mm.

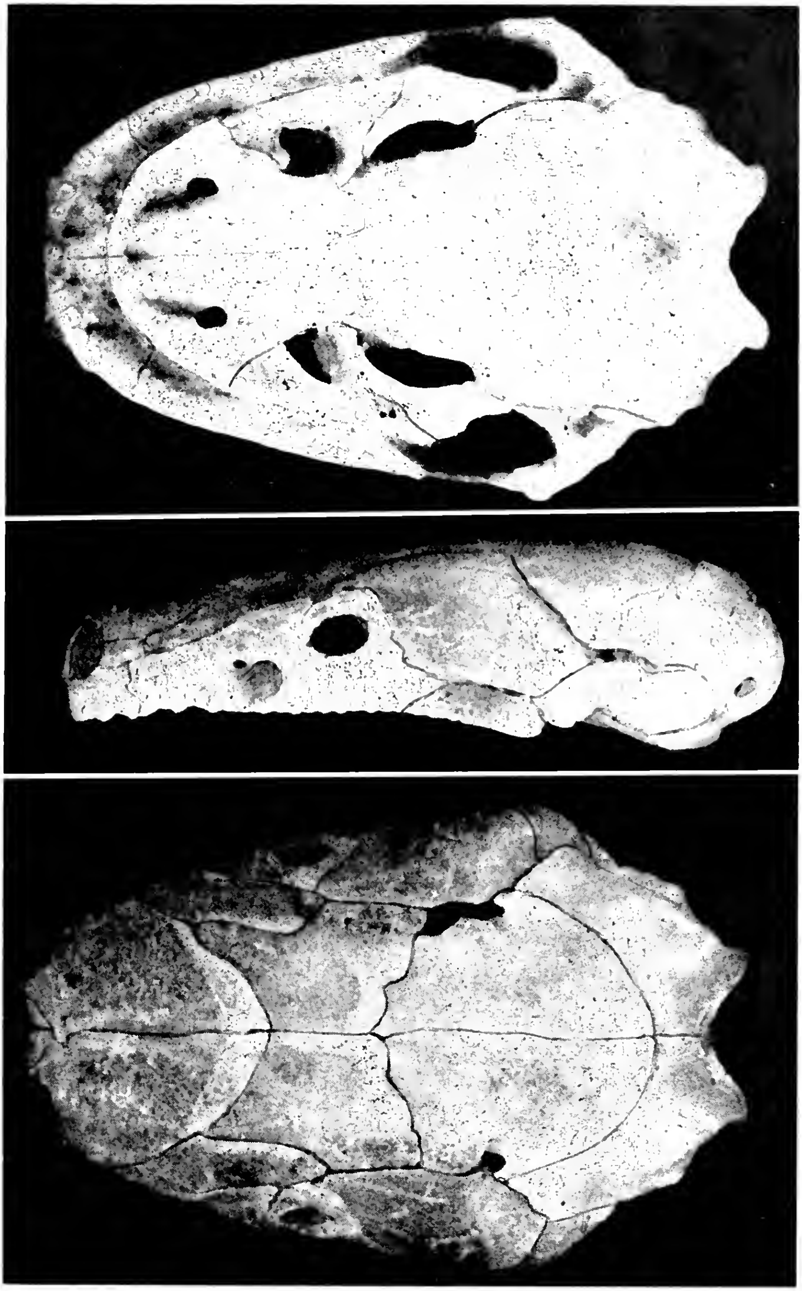

FIG. 9. *Caudacaecilia asplenia* Taylor. EHT-HMS Coll. No. 1373, LaDoo Tin Mine, Yala Province, Thailand. Total length of specimen, 238 mm; length of skull, 9.5 mm; width of skull, 6.3 mm.

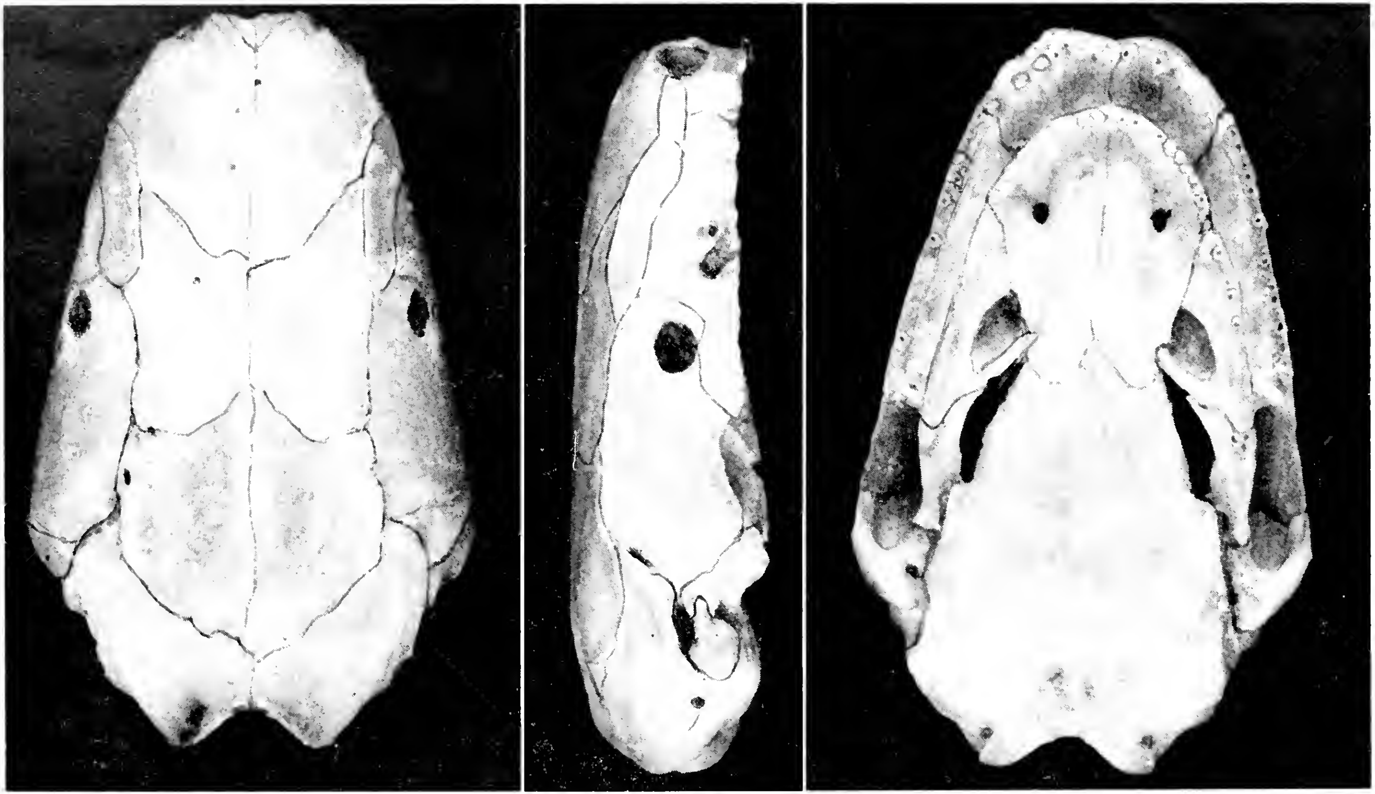

FIG. 10. *Caudacaecilia larutensis* (Taylor). EHT-HMS Coll. No. 3359, Maxwells Hill, Larut Hills, Perak, Malaya. Total length of specimen, 252 mm; length of skull, 11.0 mm; width of skull, 6.8 mm.

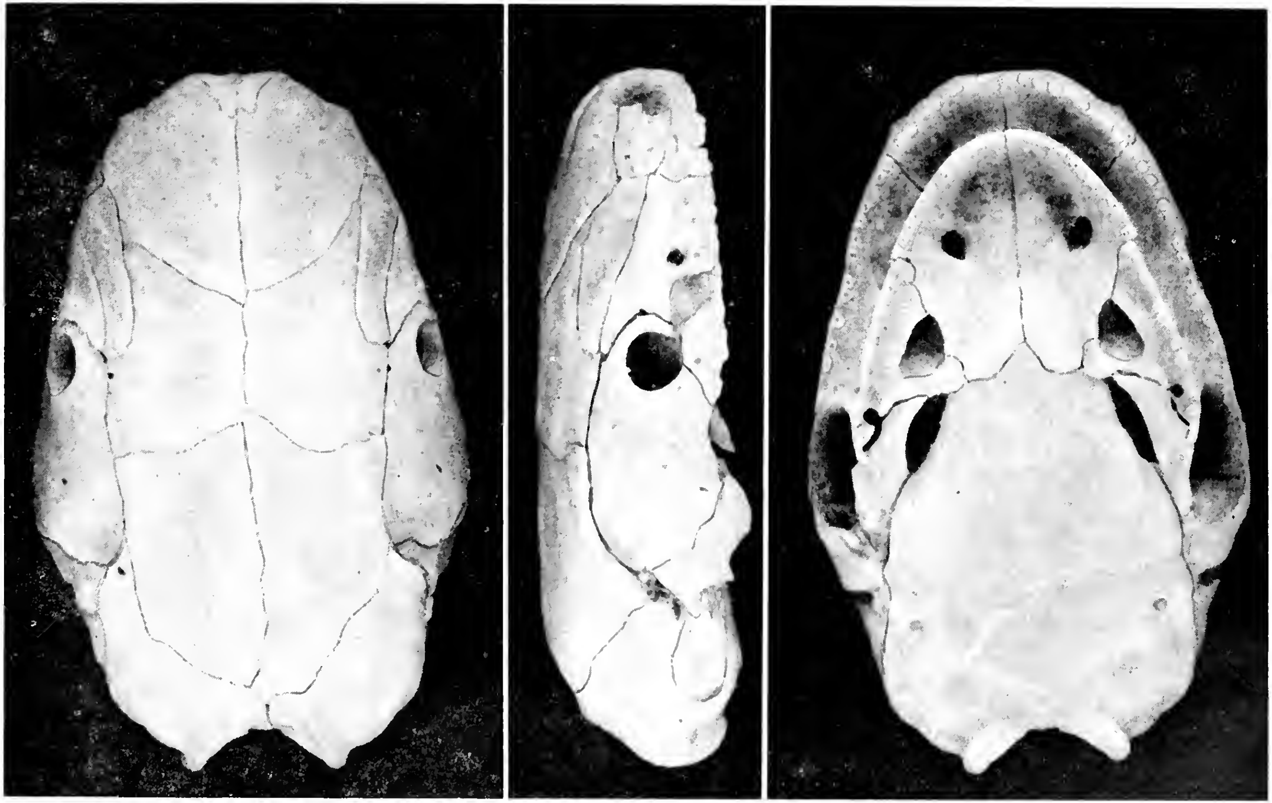

FIG. 11. *Caudacaecilia weberi* (Taylor). DSBM No. 21764. Near Malatgan River, Palawan, P.I. (paratype of the neotype). Total length of specimen, 209 mm; length of skull, 9.0 mm; width of skull, 5.4 mm.

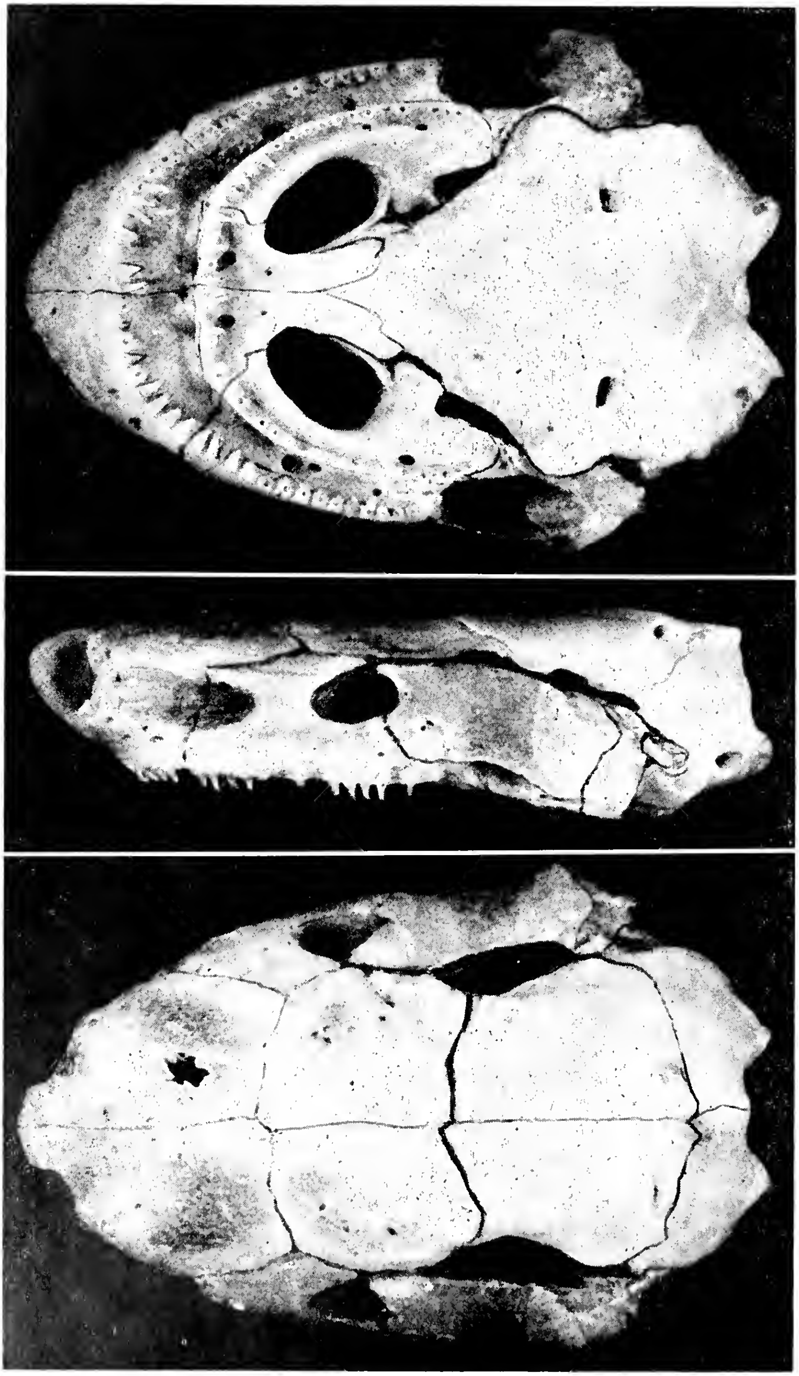

FIG. 12. *Typhlonectes compressicaudus* (Duméril and Bibron. EHT-HMS Coll. No. 1731, Belém, Brasil. Total length of specimen, 432 mm; length of skull, 16.5 mm; width of skull, 11.2 mm.

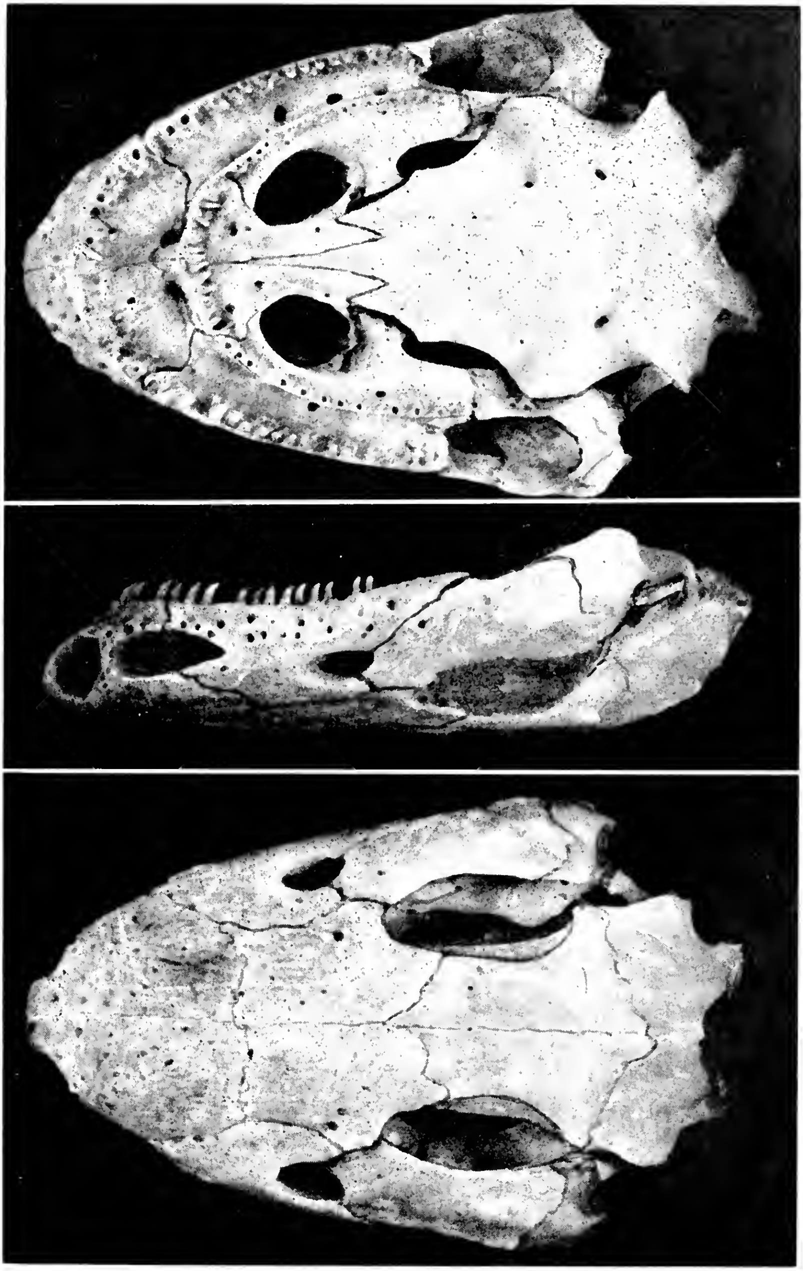

FIG. 13. *Typhlonectes natans* Fischer, *in* Peters. MCZ No. 24524, Cúcuta, Colombia. Total length of specimen, 650 mm; length of skull, 22.4 mm; width of skull, 14.8 mm.

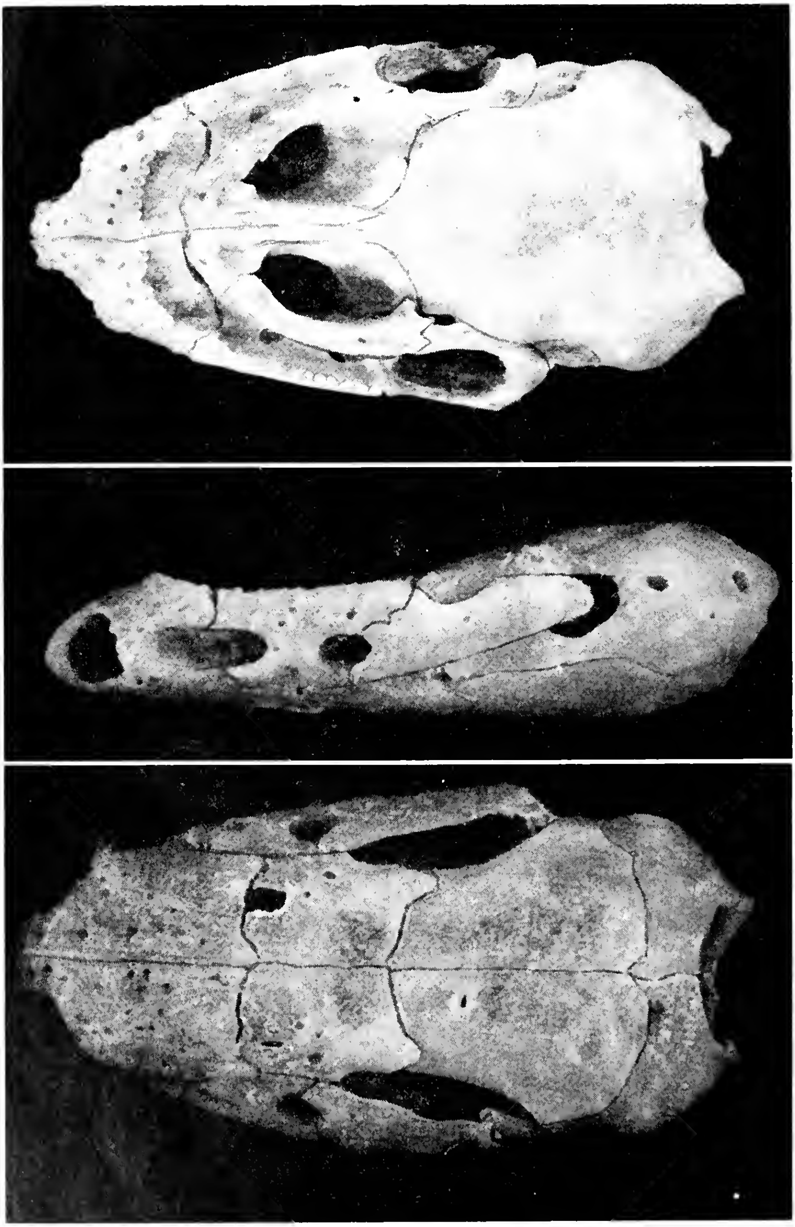

FIG. 14. *Potamotyphlus kaupii* (Berthold). UM No. 787. Uncertain locality. Total length of specimen, 452 mm; length of skull, 11.1 mm; width of skull, 5.5 mm.

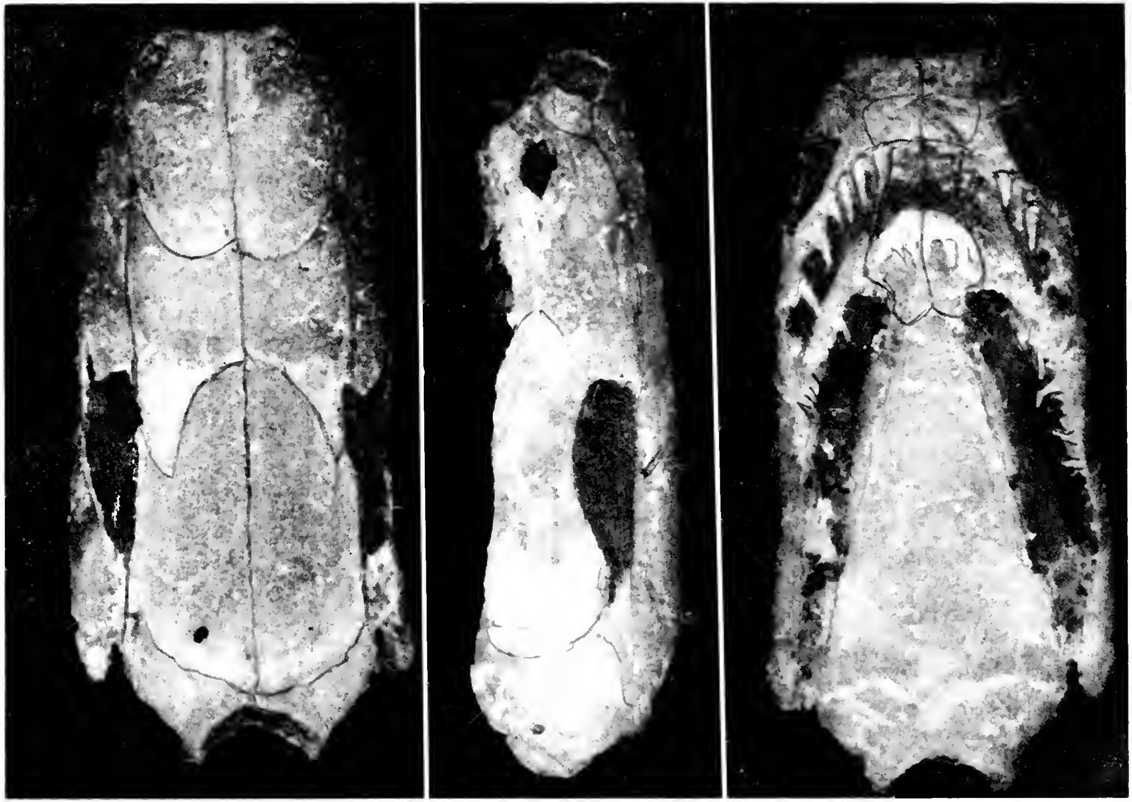

Fig. 15. *Scolecomorphus vittatus* (Boulenger). EHT-HMS Coll. No. 4642, Nyange, Vituri, Uluguru Mts., Tanganyika (Tanzania), Africa. Total length of specimen, 230± mm; length of skull, 7.25 mm; width of skull, 3.7 mm.

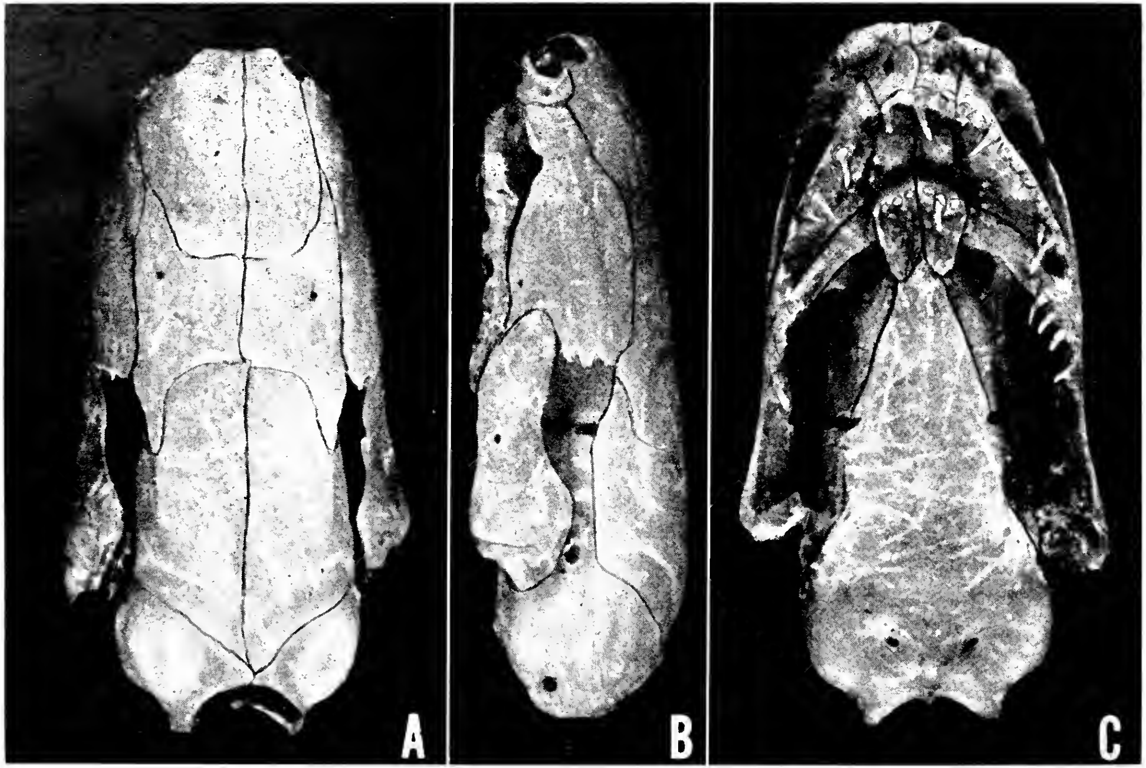

FIG. 16. *Scolecomorphus kirkii* Boulenger. MCZ No. 27120. Cholo Mts. 3600 ft. elev. Cholo district, Nyasaland (Malawi), Africa. Total length of specimen, 270 mm; length of skull, 7.9 mm; width of skull, 4.05 mm.

Fig. 17. *Caecilia nigricans* Boulenger. KUMNH No. 94377, Cana, Darién, Panamá. Total length of specimen, 1004 mm; length of skull, 21.0 mm; width of skull, 13.2 mm.

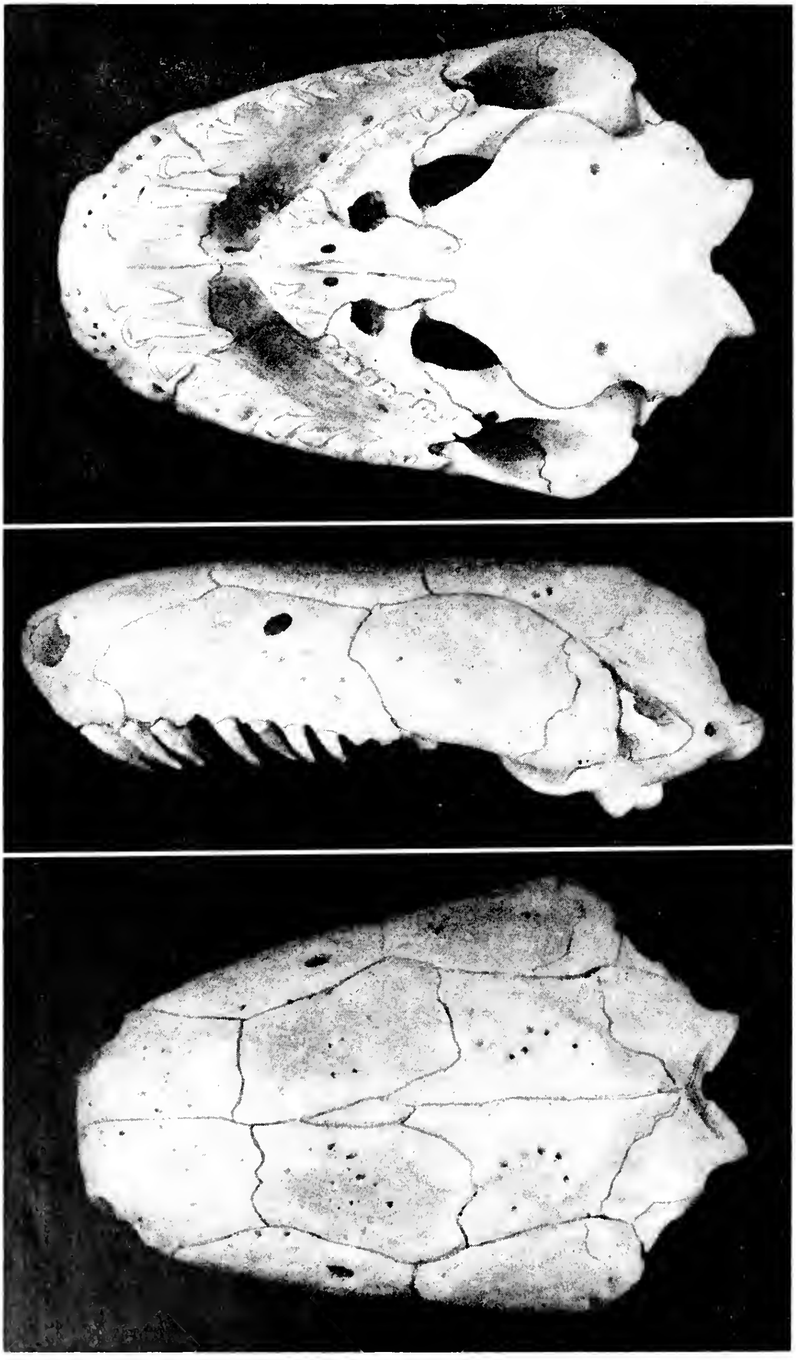

FIG. 18. *Caecilia tentaculata* Linnaeus. KUMNH No. 104438, Santa Cecilia, Napo-Pastaza, Ecuador. Total length of specimen, 790 mm; length of skull, 24.0 mm; width of skull, 16.0 mm.

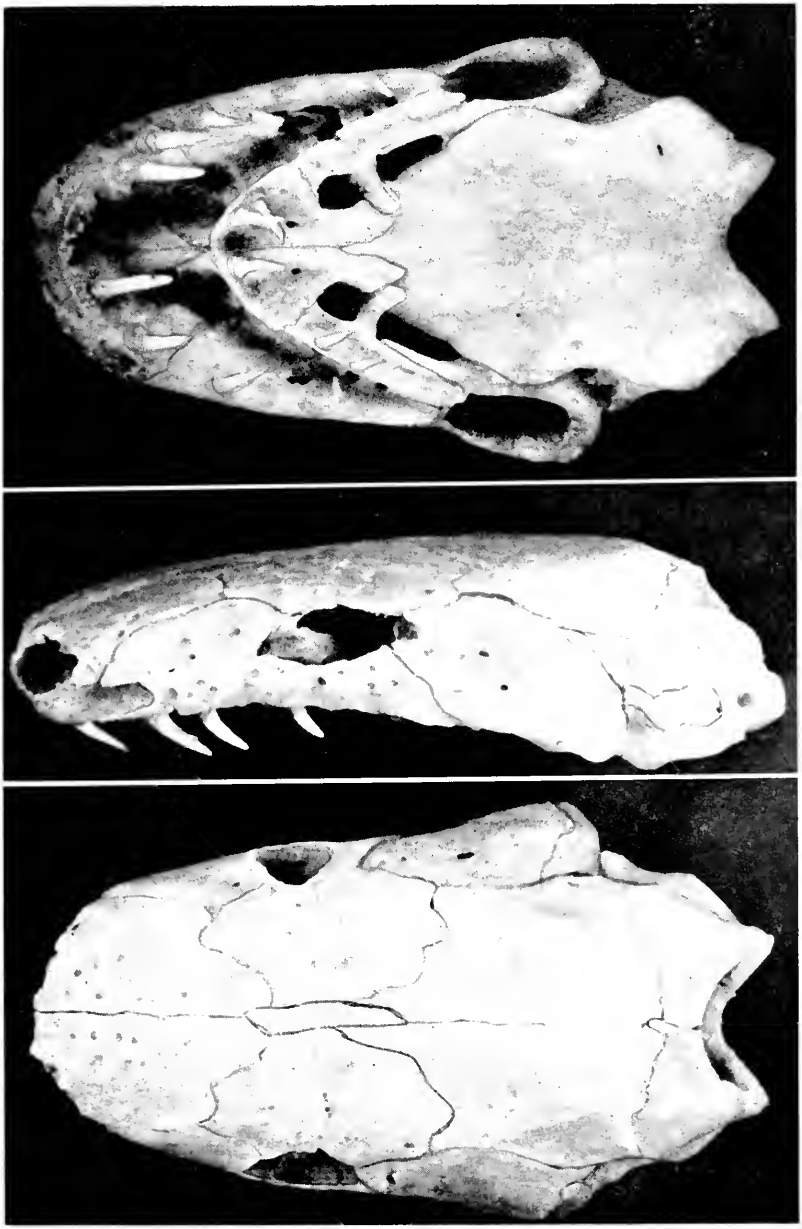

FIG. 19. *Caecilia degenerata* Dunn. AMNH No. 23354. Colombia, S.A. (no specific locality). Total length of specimen, 350 mm; length of skull, 10.4 mm; width of skull, 5.8 mm.

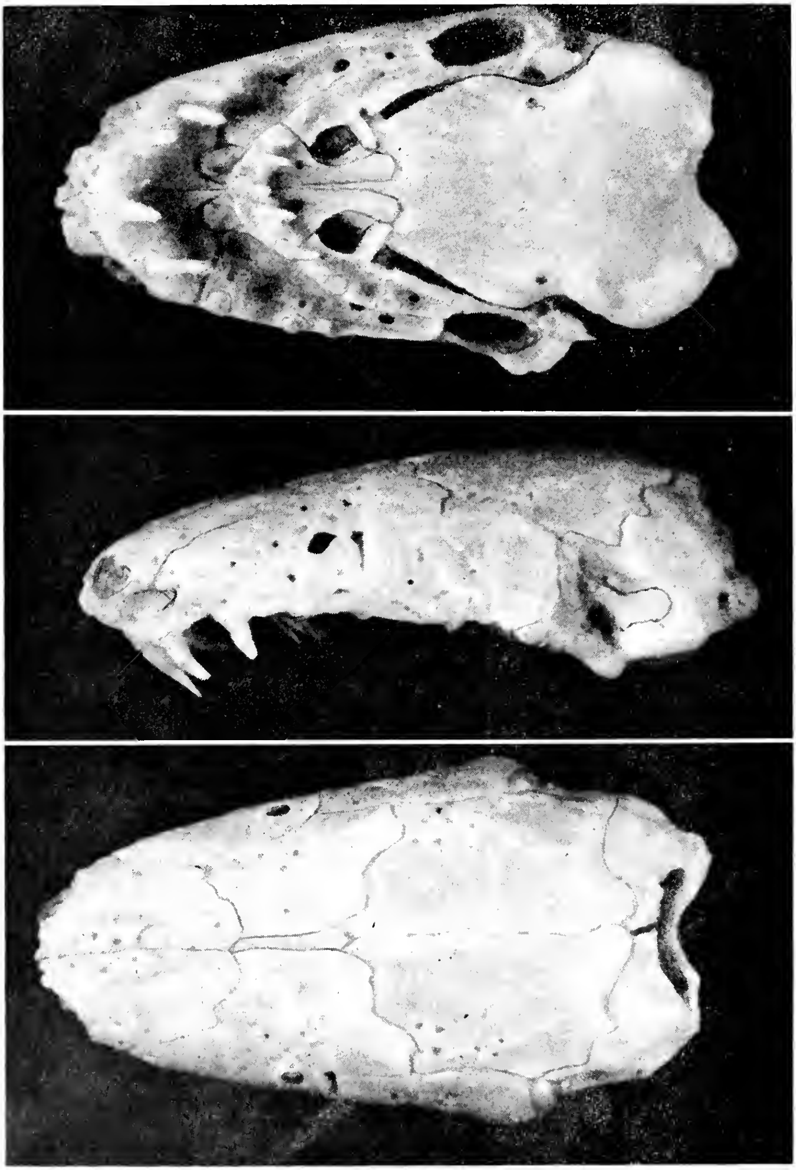

FIG. 20. *Caecilia disossea* Taylor. EHT-HMS Coll. No. 1808. Alto Cararay, Napo-Pastaza, Ecuador. Total length of specimen, 686 mm; length of skull, 6.9 mm; width of skull, 3.8 mm.

FIG. 21. *Caecilia volcani* Taylor. EHT-HMS Coll. No. 4696. Valle de Antón, Coclé, Panamá. Total length of specimen, 290 mm; length of skull, 8.5 mm; width of skull, 5.1 mm.

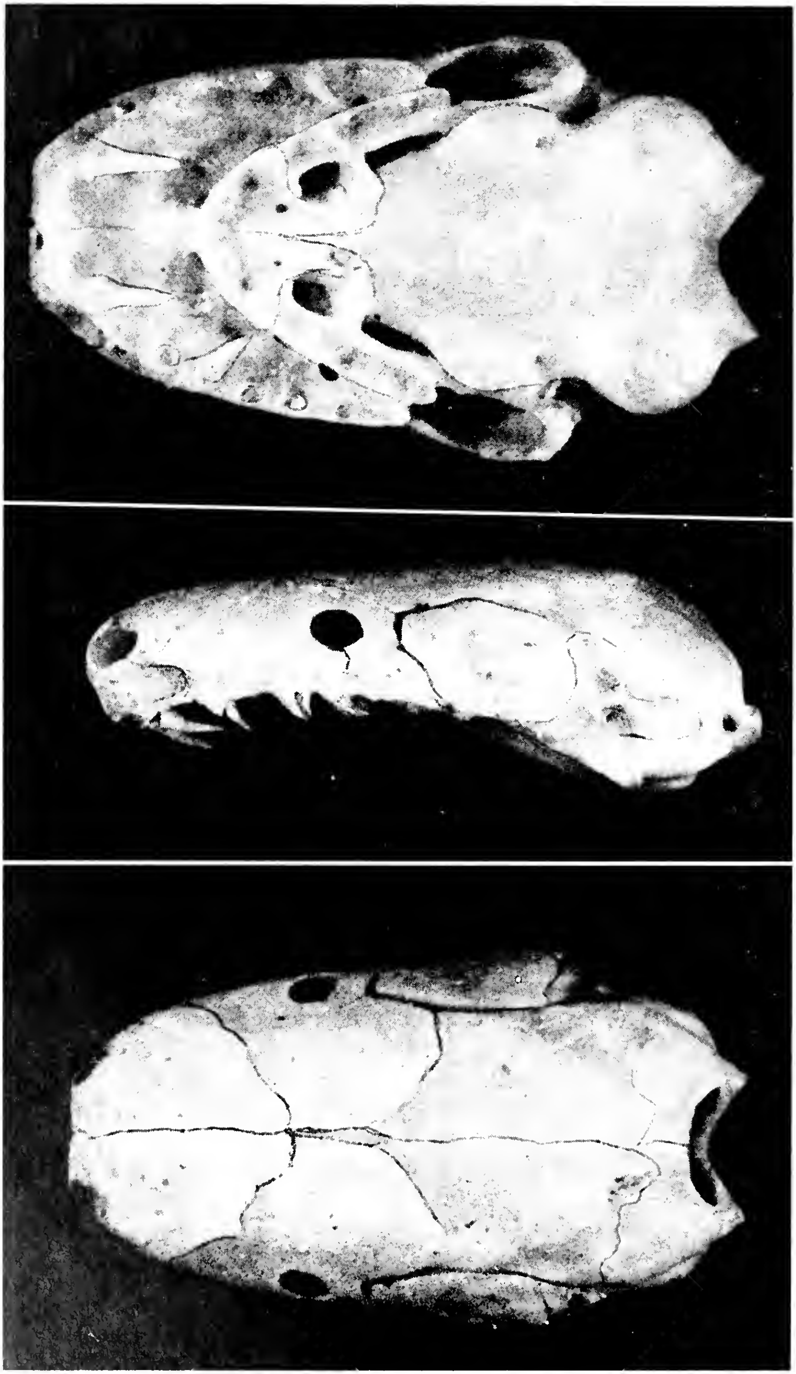

FIG. 22. *Caecilia orientalis* Taylor. EHT-HMS Coll. No. 4677, "Ecuador." Total length of specimen, 337 mm; length of skull, 9.0 mm; width of skull, 5.2 mm.

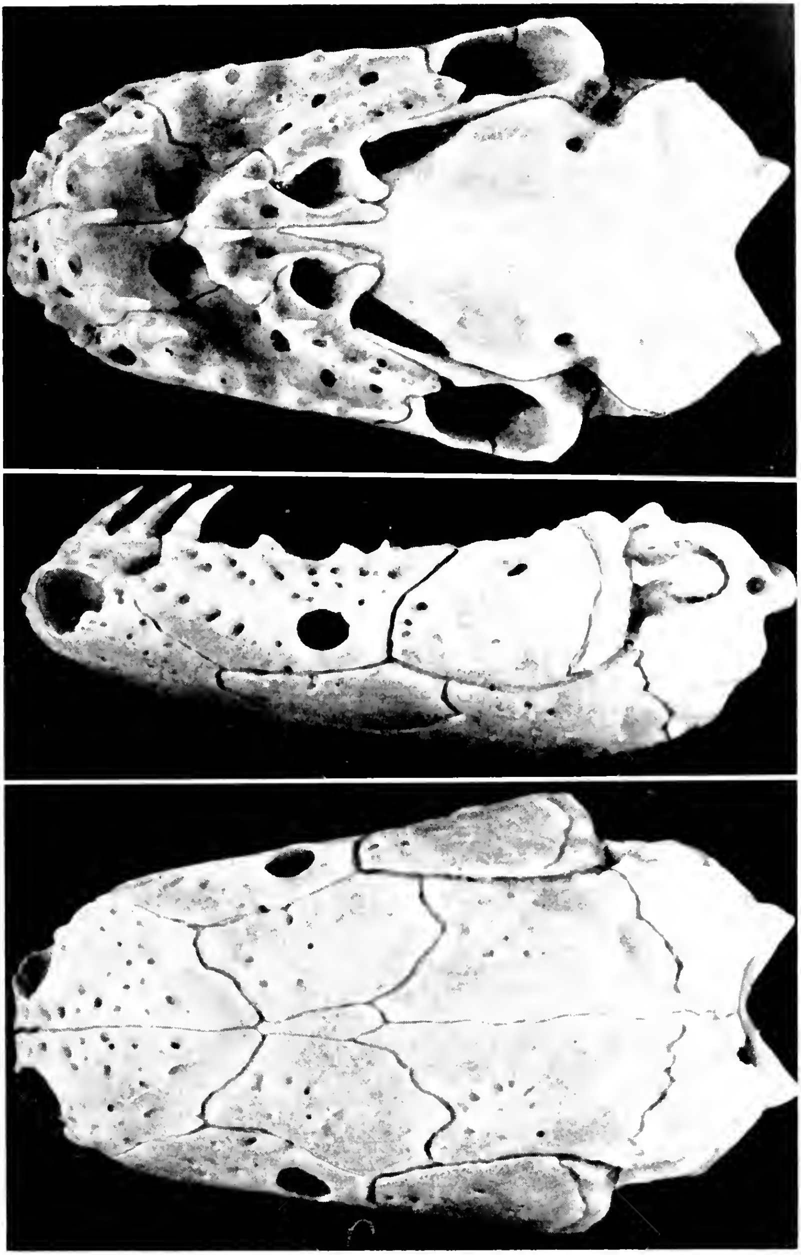

FIG. 23. *Caecilia albiventris* Daudin. AMNH No. 49960, "Bogota!" Colombia. Total length of specimen, 278 mm; length of skull, 10.3 mm; width of skull, 5.9 mm.

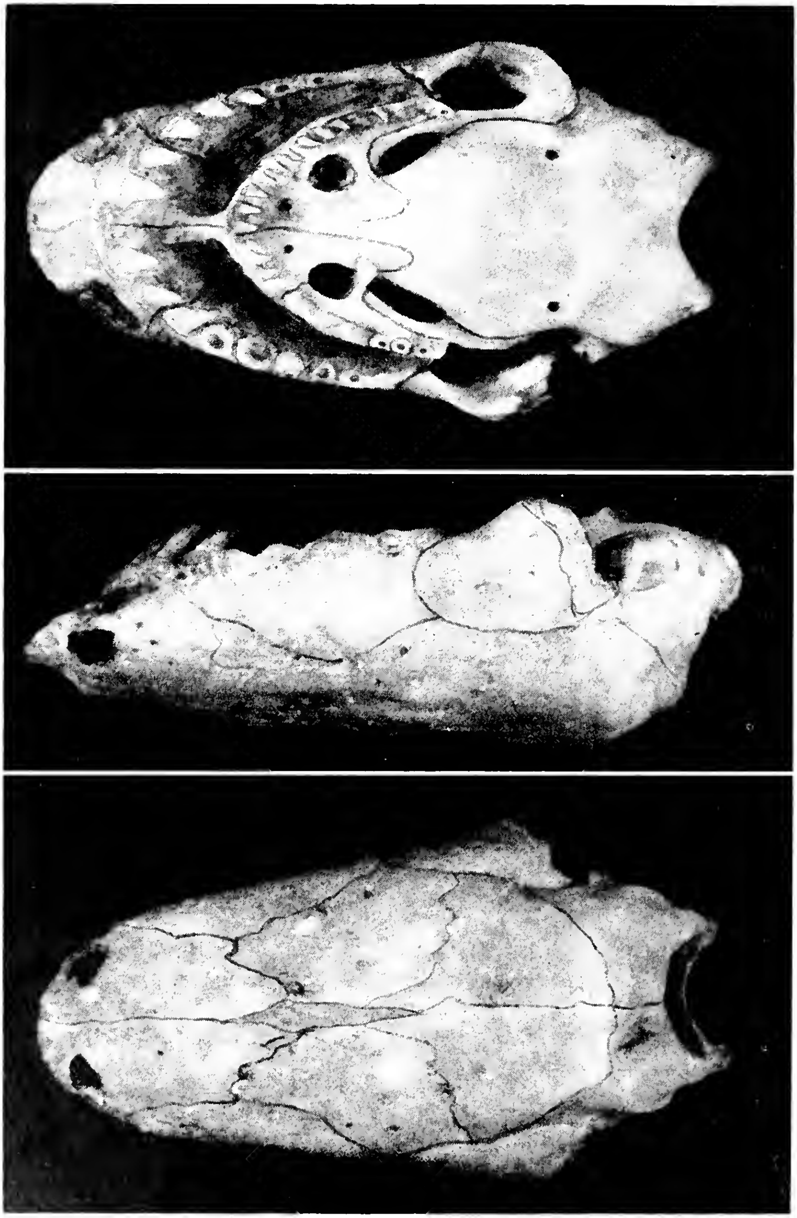

FIG. 24. *Oscaecilia ochrocephala* (Cope). MCZ No. 14817, Ancón, Canal Zone, Panamá. Total length of specimen, 542± mm; length of skull, 12.1 mm; width of skull, 6.6 mm.

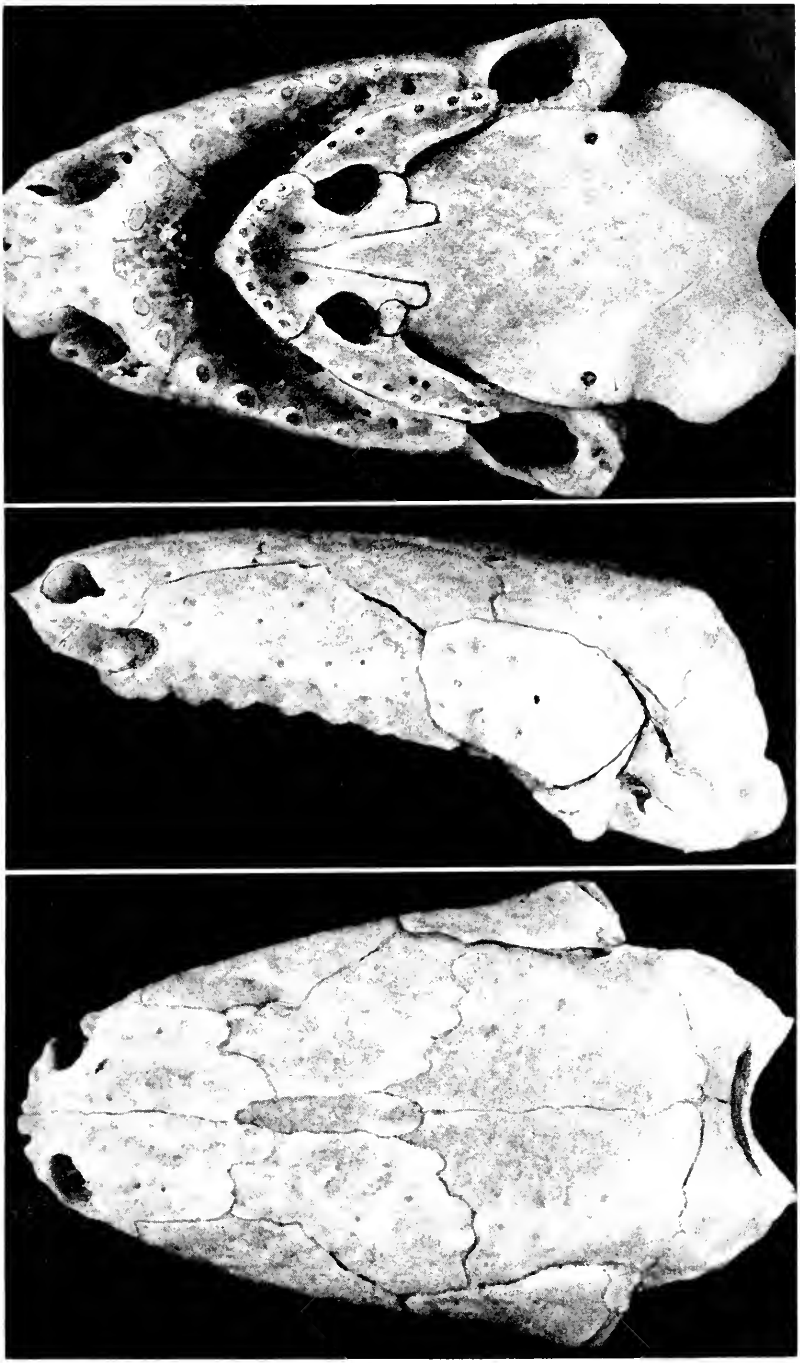

FIG. 25. *Oscaecilia ochrocephala* (Cope). UIM No. 41092, Gatun, Canal Zone, Panamá. Length of skull, 8.9 mm; width of skull, 5.2 mm.

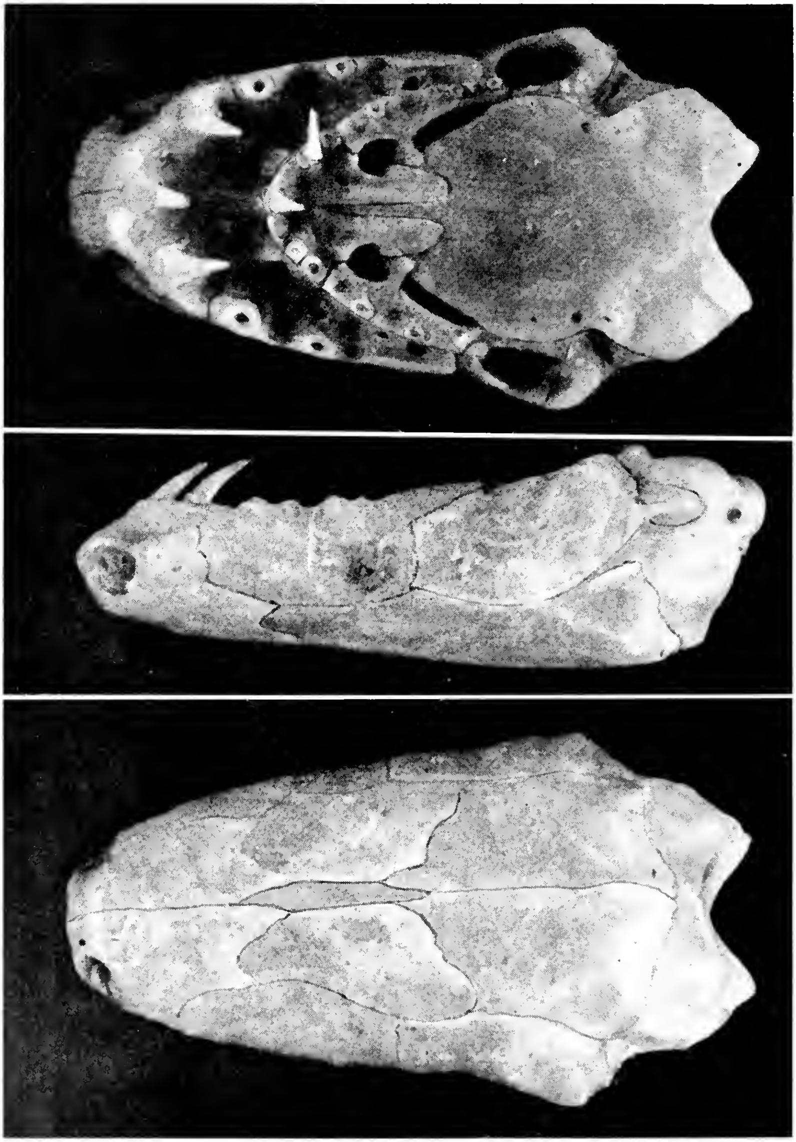

FIG. 26. *Oscaecilia bassleri* (Dunn). EHT-HMS Coll. No. 4675, "Ecuador." Total length of specimen, 890± mm; length of skull, 9.0 mm; width of skull, 4.8 mm.

FIG. 27. *Dermophis eburatus* Taylor. MCZ No. 12121, Guatemala, C.A. Total length of specimen, 419 mm; length of skull, 20.0 mm; width of skull, 14.5 mm.

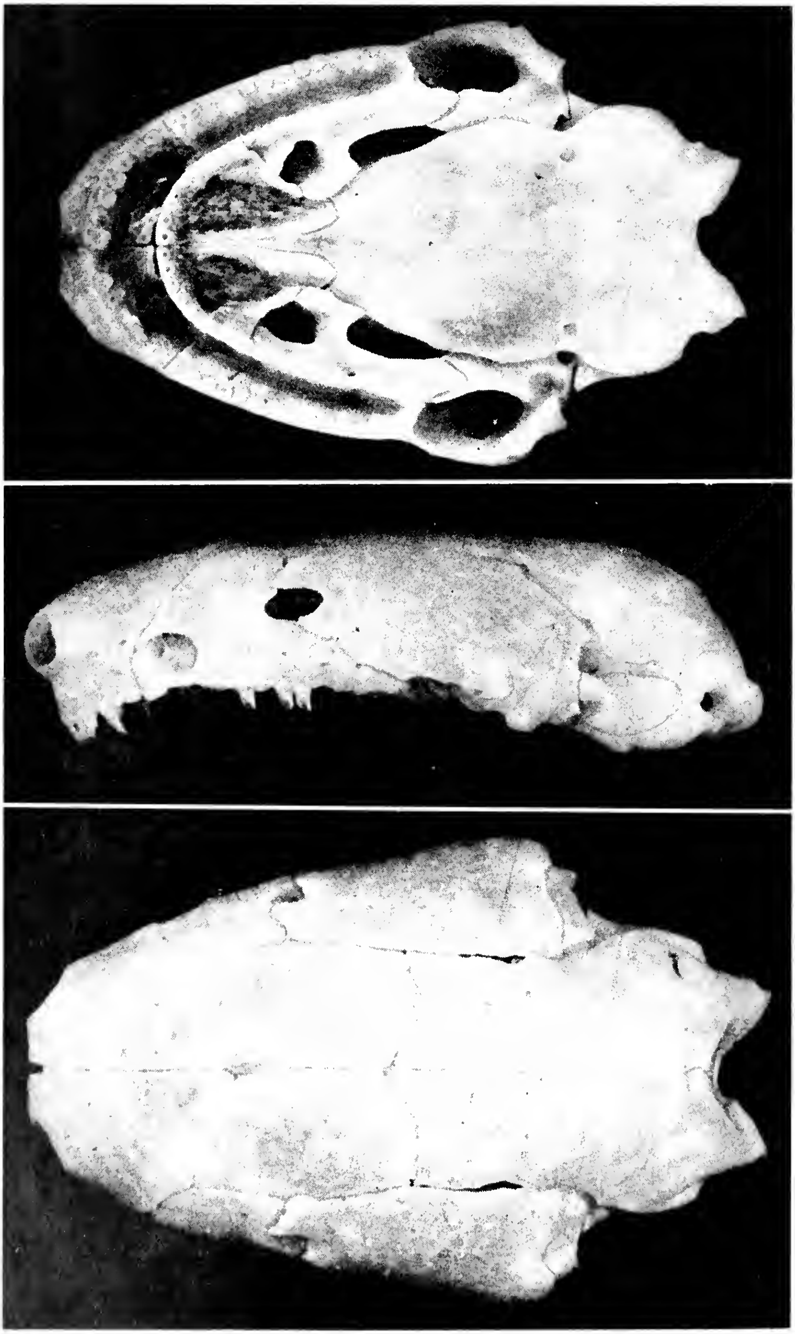

FIG. 28. *Dermophis costaricensis* Taylor. KUMNH No. 66805, Moravia, Cartago Prov., Costa Rica. Total length of specimen, 344 mm; length of skull, 13.5 mm; width of skull, 8.5 mm.

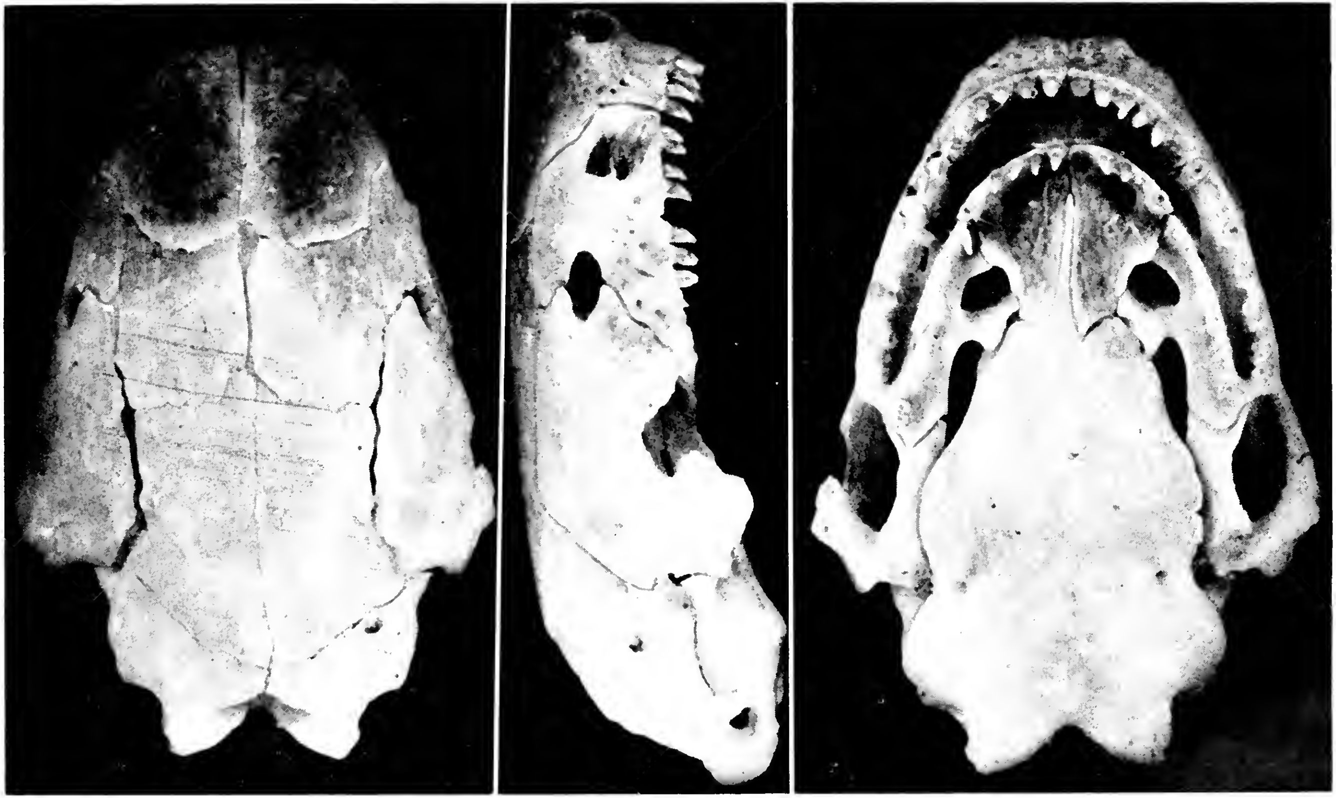

FIG. 29. *Dermophis balboai* Taylor. KUMNH No. 108935, Darién, Panamá. Total length of specimen, 356 mm; length of skull, 14.05 mm; width of skull, 9.5 mm.

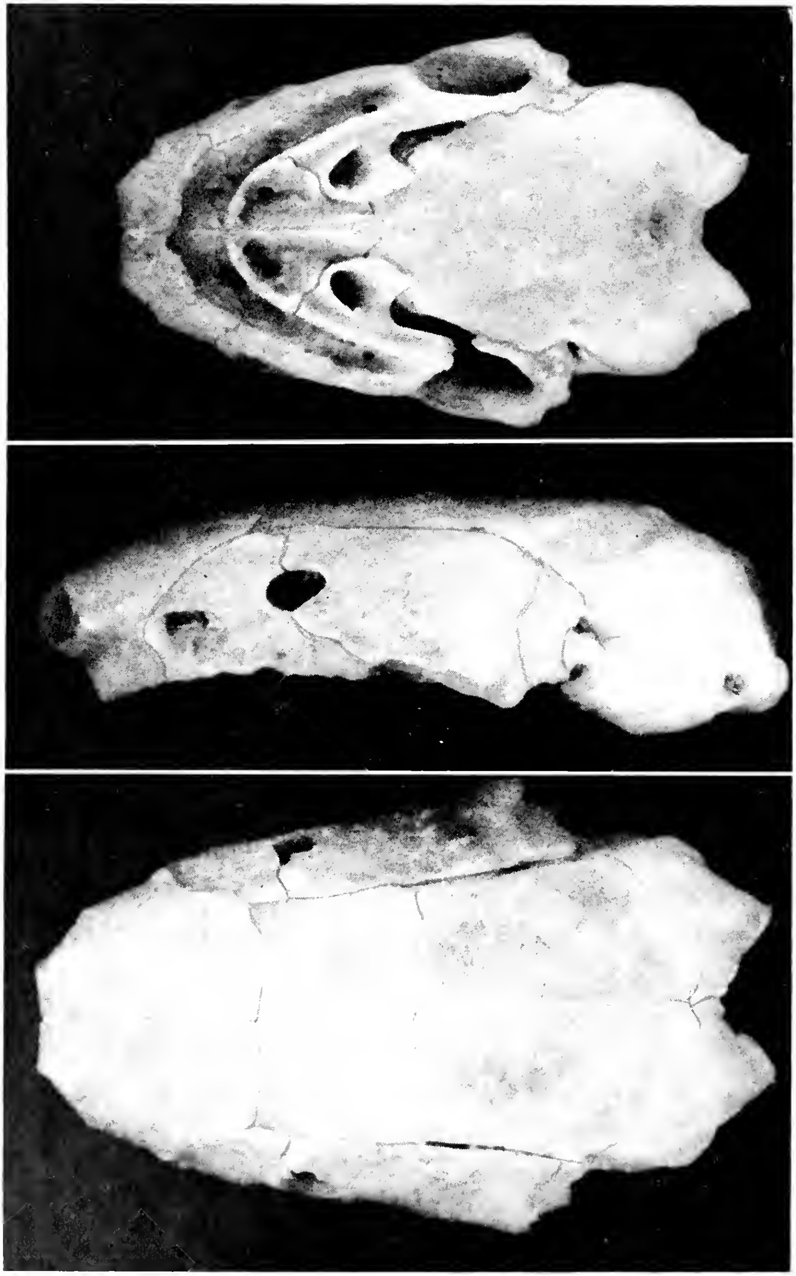

FIG. 30. *Dermophis parviceps* (Dunn). KUMNH No. 36276, Cartago, Costa Rica. Total length of specimen, 193 mm; length of skull, 8.2 mm; width of skull, 5.0 mm.

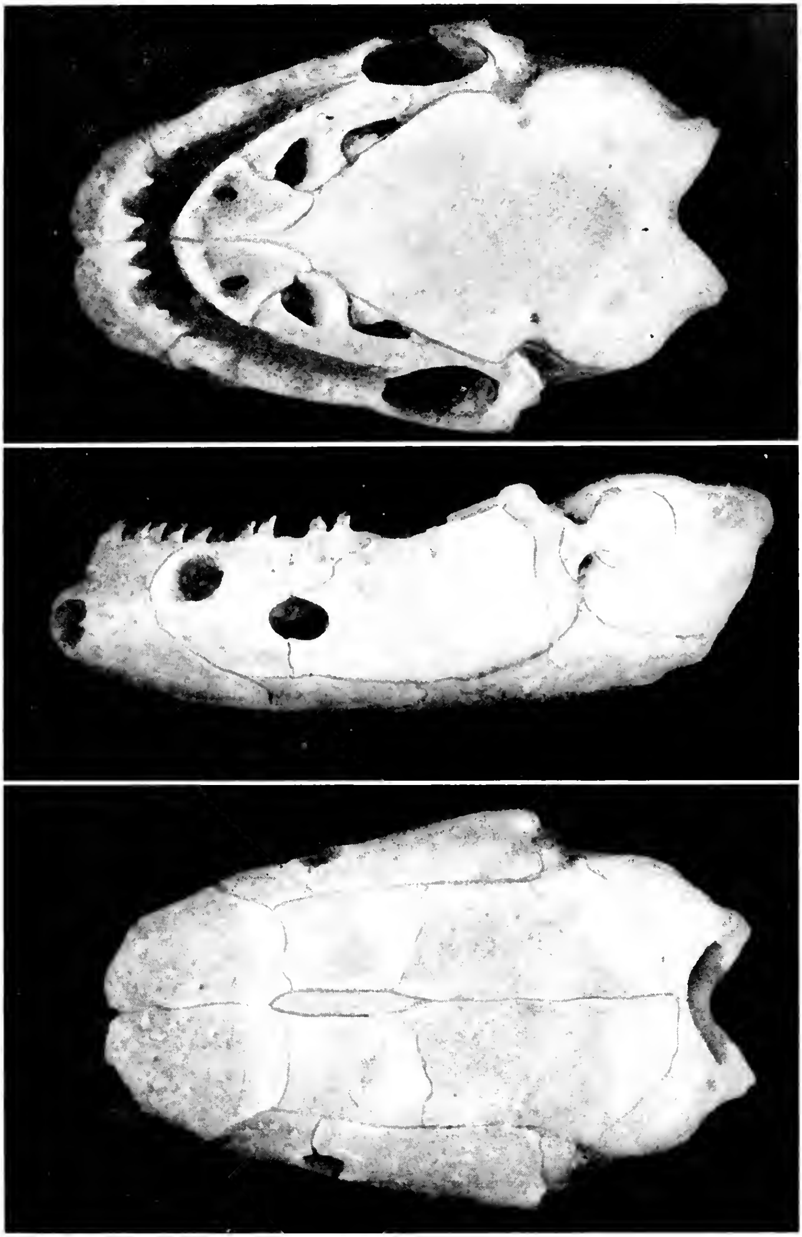

Fig. 31. *Dermophis glandulosus* Taylor. KUMNH No. 56070, San Isidro del General, San José Prov., Costa Rica. Total length of specimen, 180 mm; length of skull, 8.85 mm; width of skull, 6.4 mm.

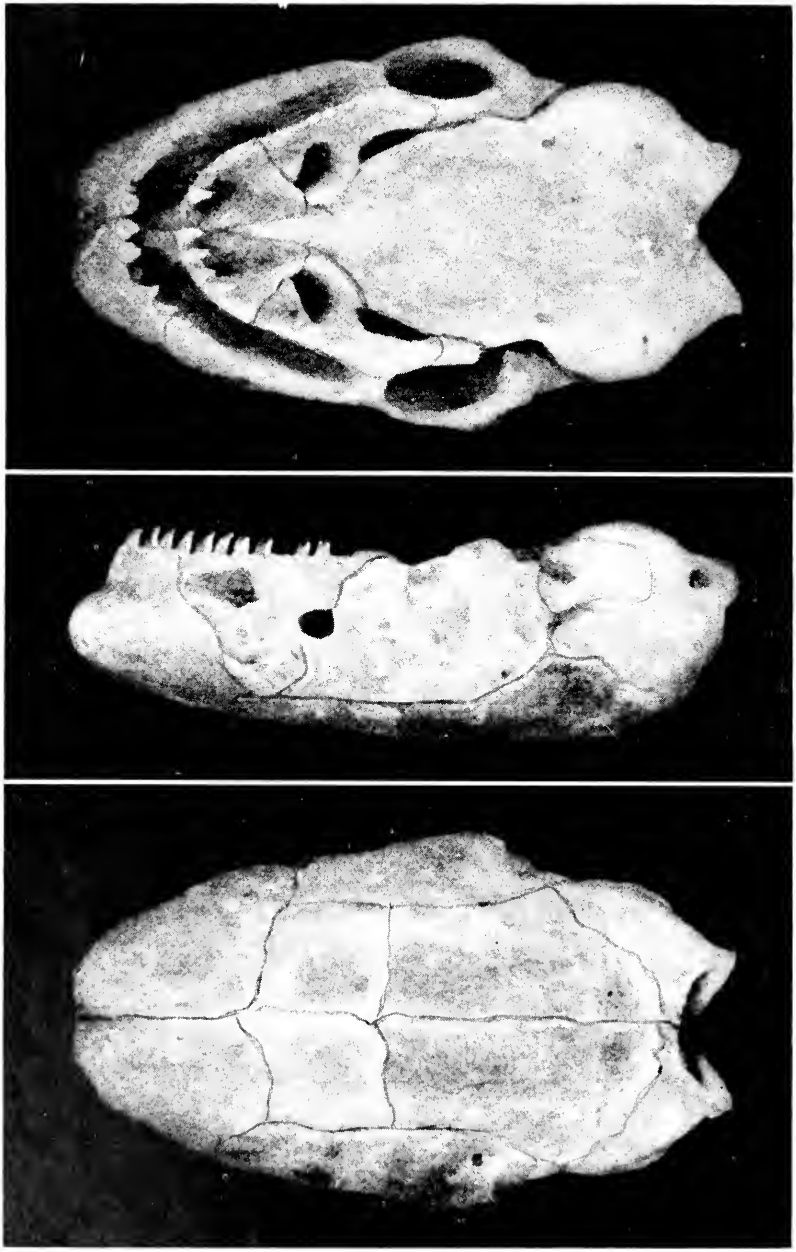

FIG. 32. *Dermophis occidentalis* Taylor. KUMNH No. 36296, "between San Isidro del General and Dominical." Total length of specimen, 194 mm; length of skull, 6.75 mm; width of skull, 4.0 mm.

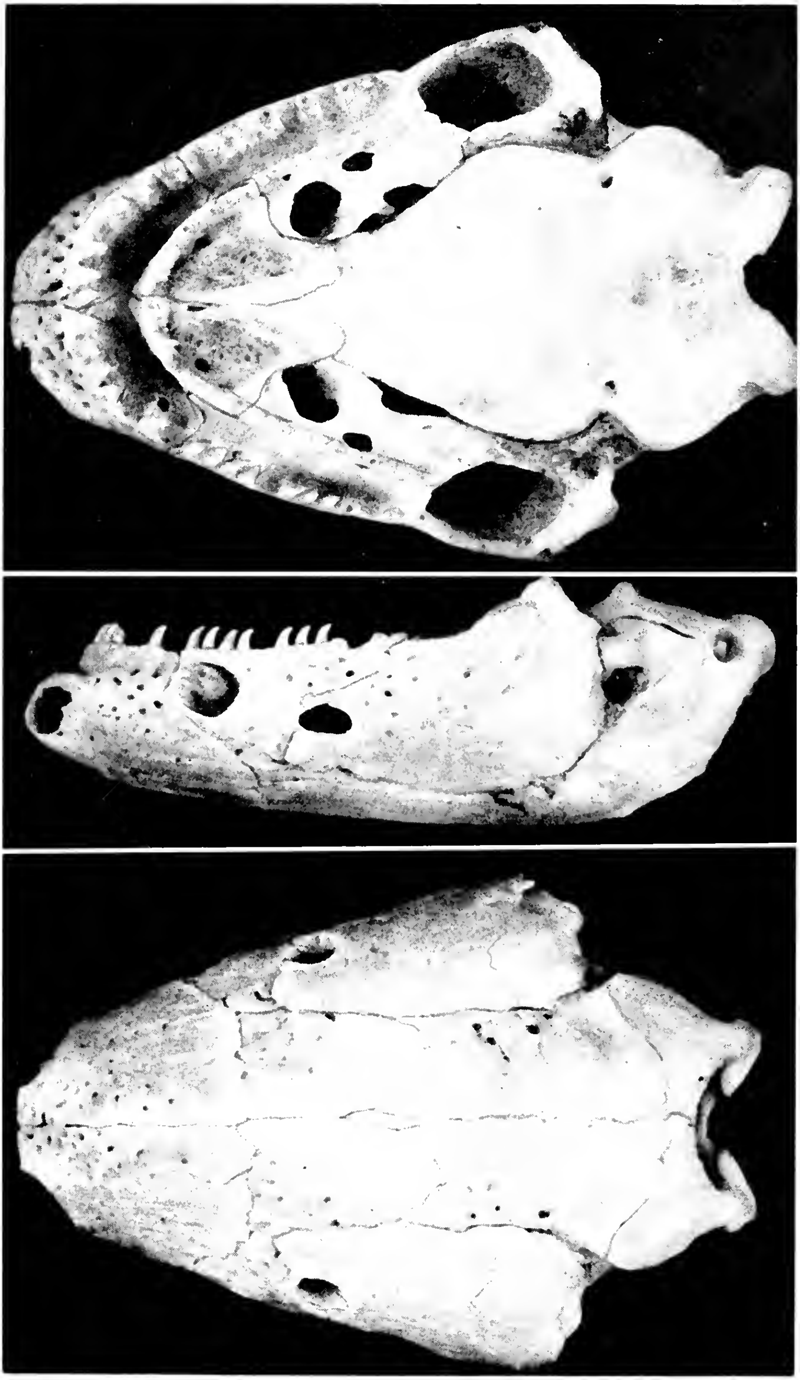

FIG. 33. *Dermophis mexicanus mexicanus* (Duméril and Bibron). UIM No. 66889, Chiapas, Mexico. Total length of specimen, 402 mm; length of skull, 16.3 mm; width of skull, 10.6 mm.

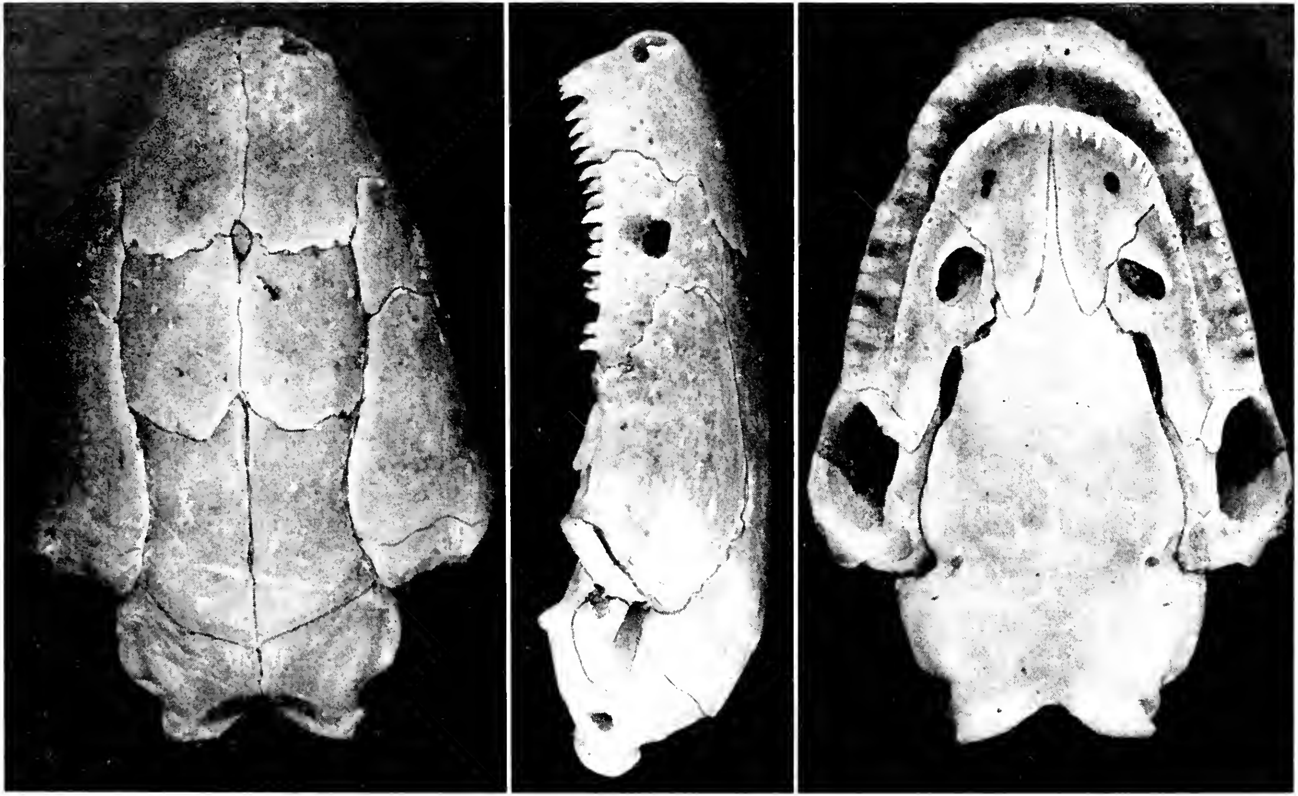

FIG. 34. *Gymnopis multiplicata* Peters. EHT-HMS Coll. No. 4702, San Bosco (Rancho), Tilarán, Guanacaste, Costa Rica. Total length of specimen, 430 mm; length of skull, 16.0 mm; width of skull, 10.8 mm.

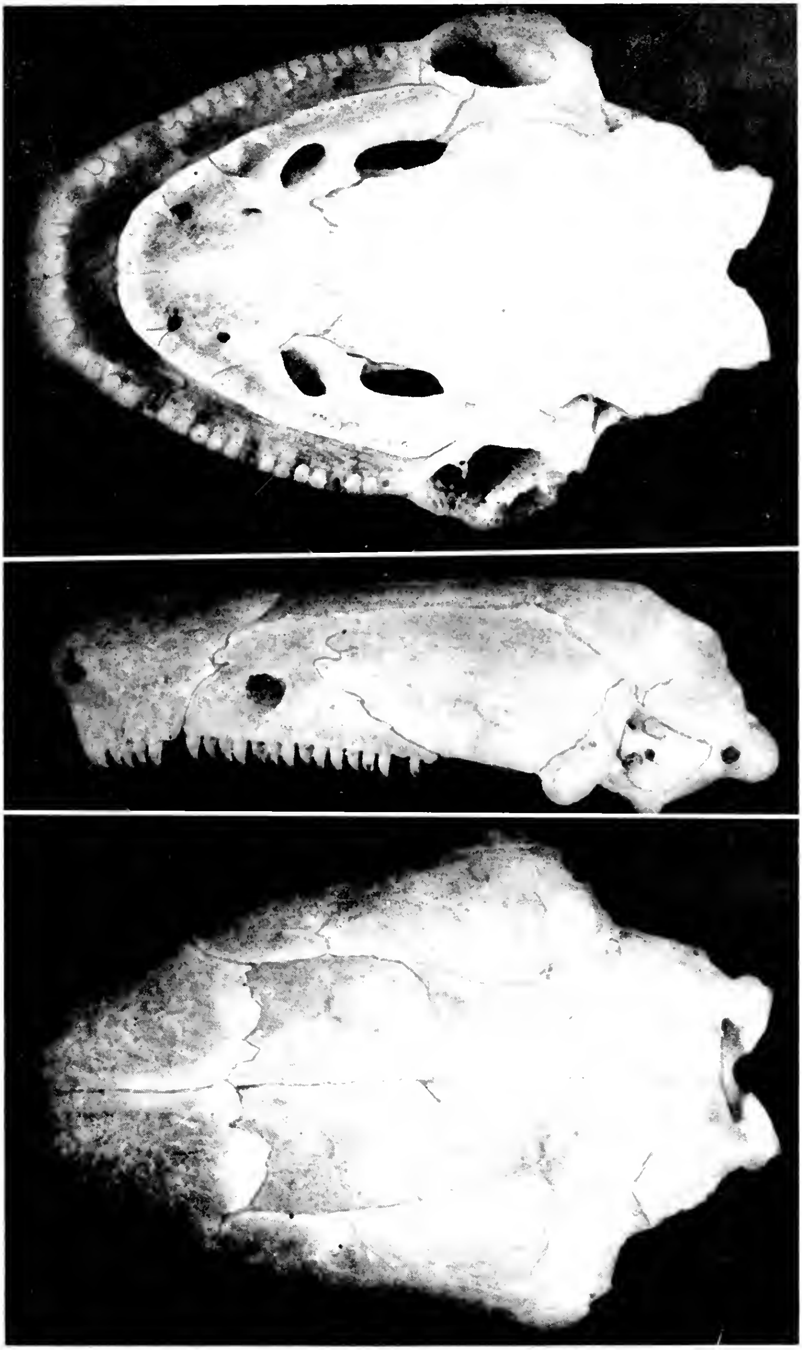

FIG. 35. *Gymnopis proxima* (Cope). EHT-HMS Coll. No. 4712, Dominica (Rancho), Turrialba, Cartago, Costa Rica. Total length of specimen, 459 mm; length of skull, 16.85 mm; width of skull, 11.6 mm.

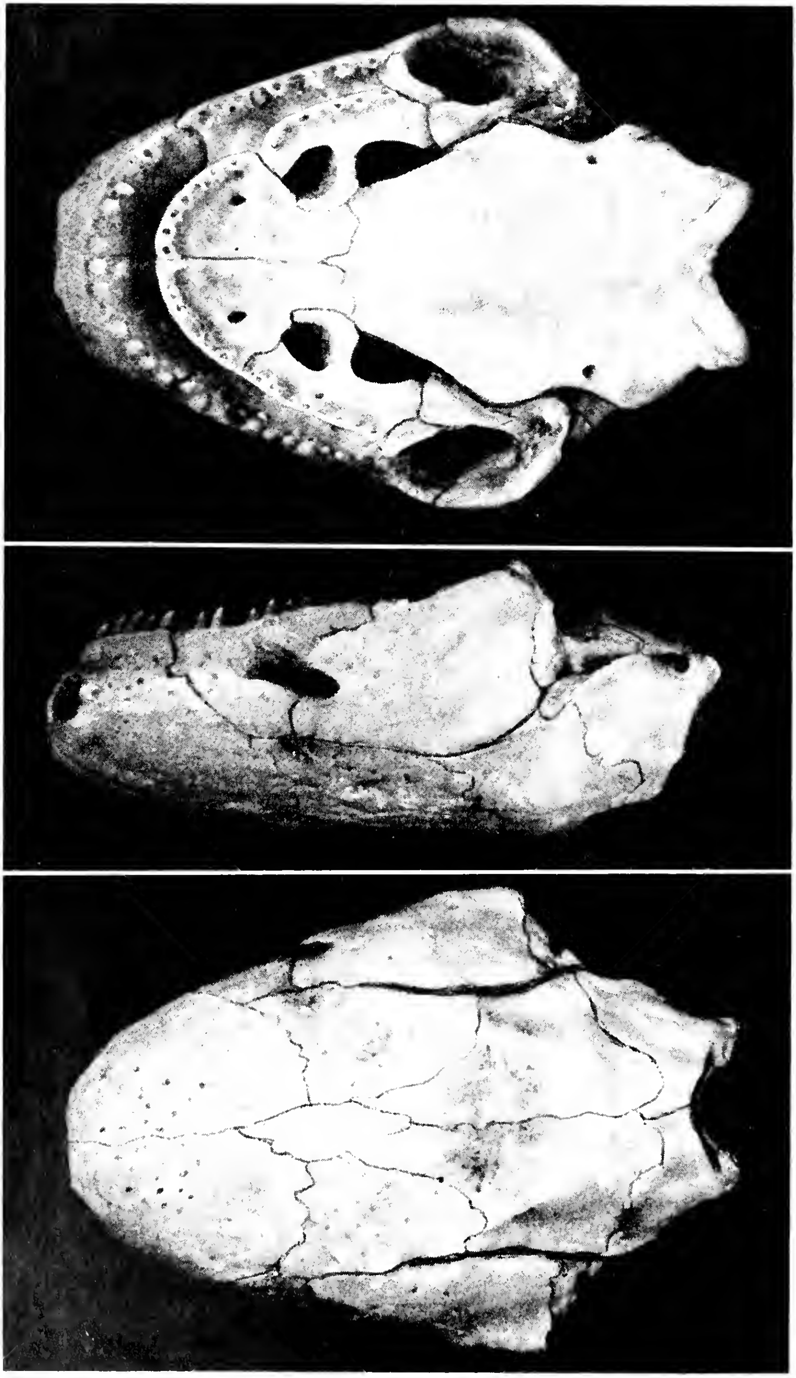

FIG. 36. *Siphonops annulatus* (Mikan). MCZ No. 19407, "Pastaza River to Marañon," Ecuador. Total length of specimen, 356 mm; length of skull, 15.4 mm; width of skull, 11.0 mm.

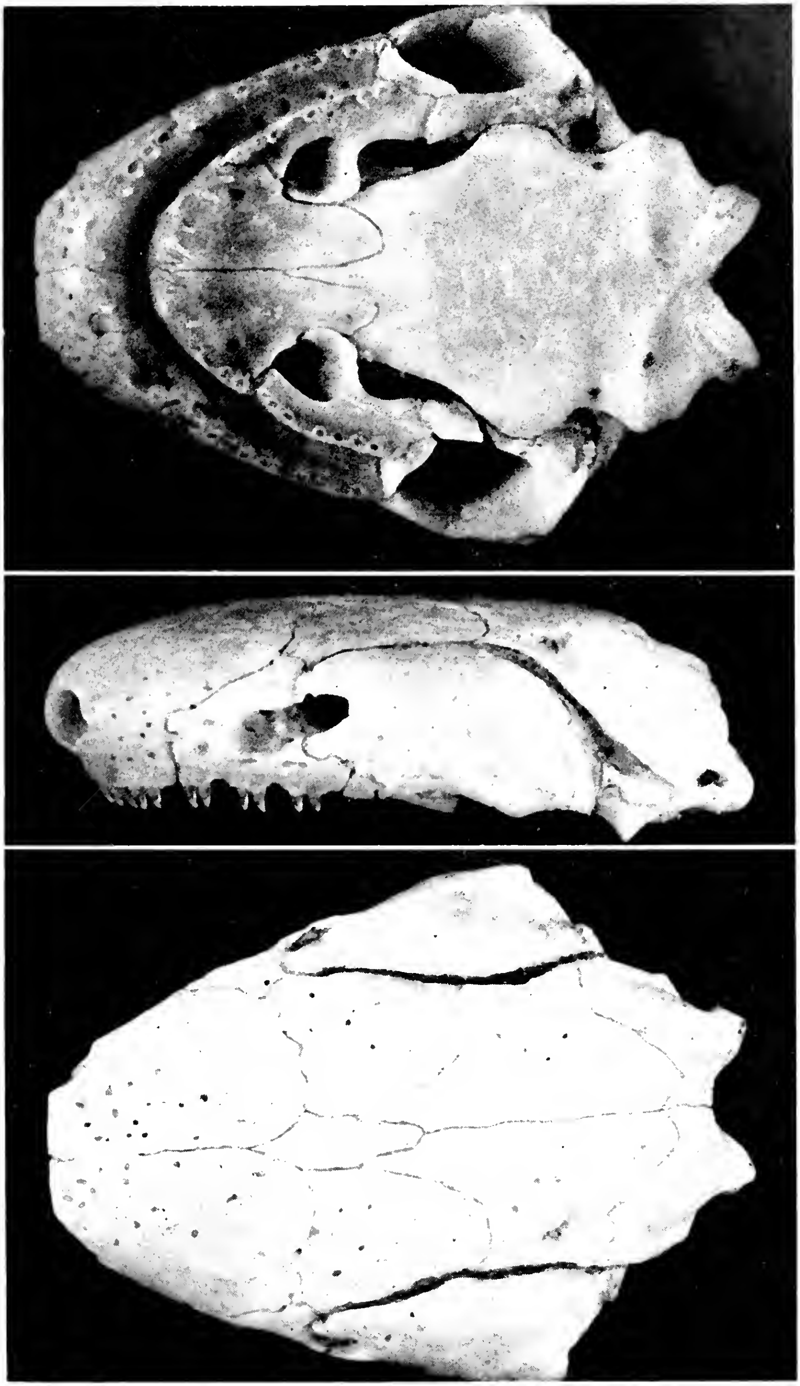

Fig. 37. *Siphonops annulatus* (Mikan). UIM No. 56668, Limón Cocha, Ecuador. Total length of specimen, 397 mm; length of skull, 15.4 mm; width of skull 11.2 mm.

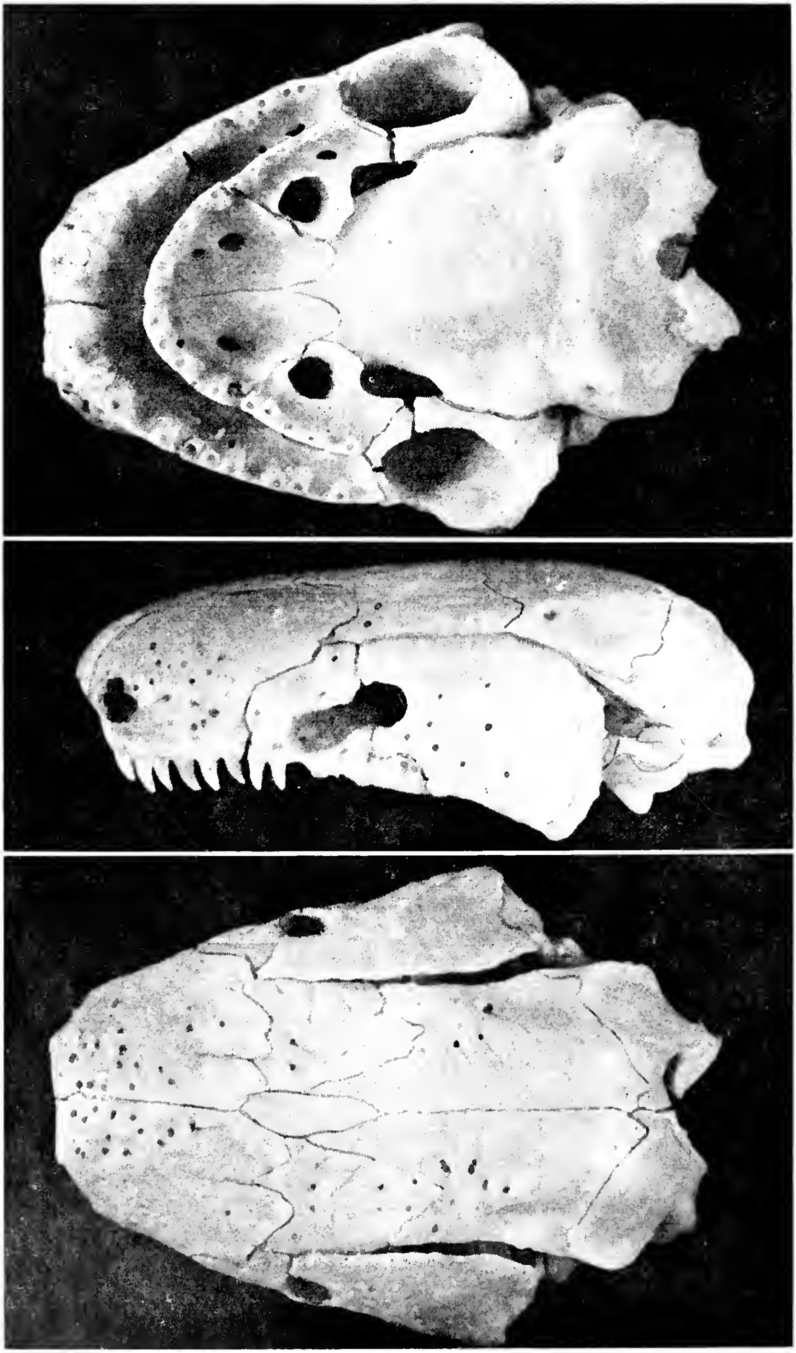

FIG. 38. *Siphonops annulatus* (Mikan). EHT-HMS Coll. No. 1848, Teresopolis, Guanabara, Brasil. Length of skull, 13.0 mm; width of skull, 9.4 mm.

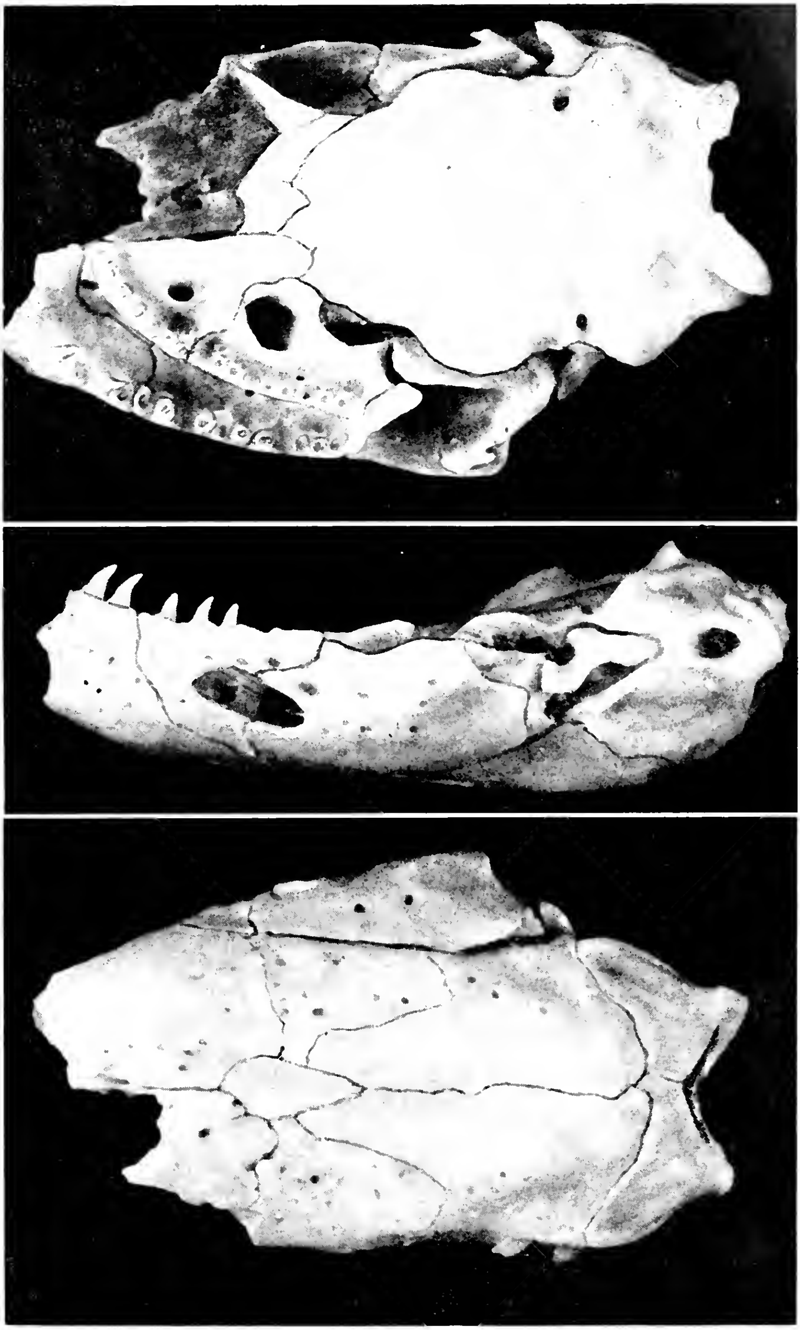

FIG. 39. *Siphonops paulensis* Boettger. AMNH No. 23433, "Brasil." Total length of specimen, 453 mm; length of skull, 13.7 mm; width of skull, 9.55 mm. (Left side of skull badly broken.)

FIG. 40. *Geotrypetes seraphini seraphini* A. Duméril. MCZ No. 3424, Metet, Cameroons. Total length of specimen, 288 mm; length of skull, 9.0 mm; width of skull, 6.0 mm.

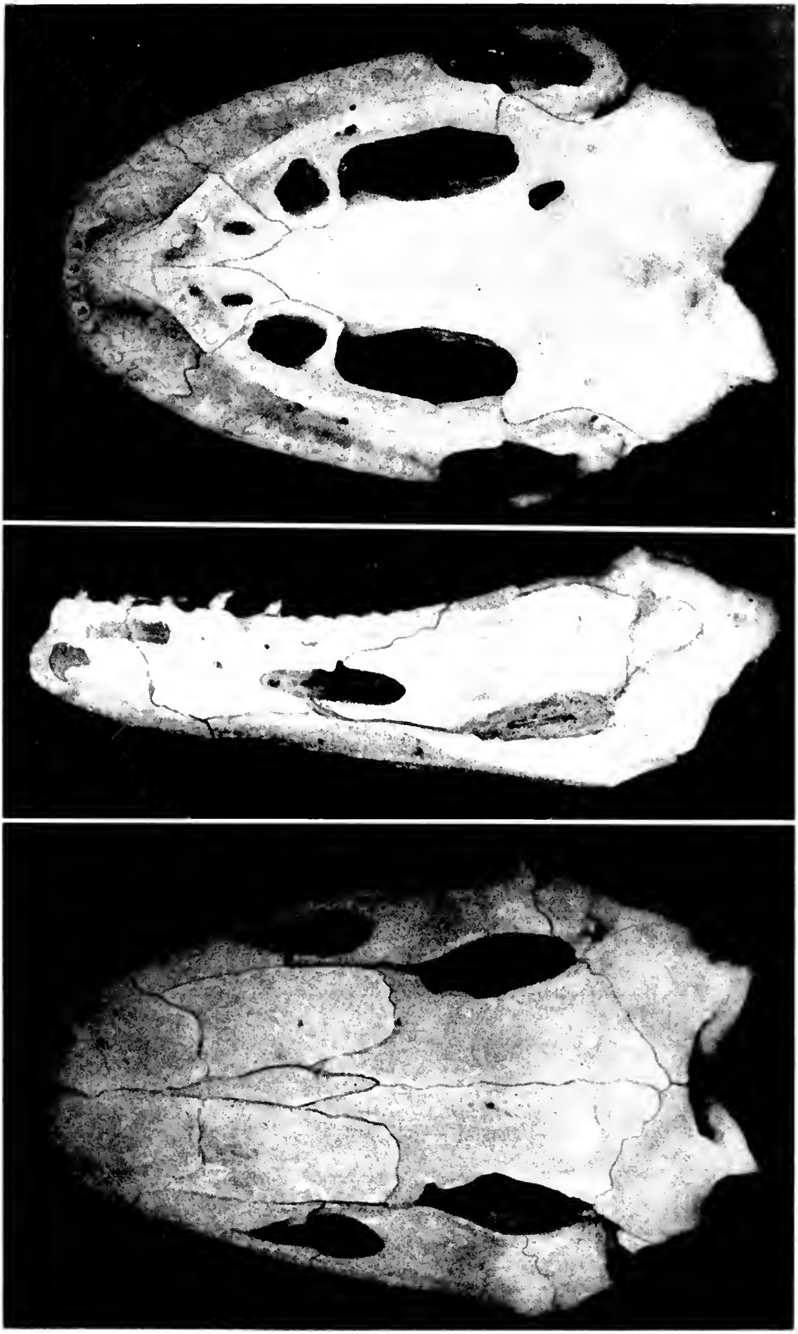

FIG. 41. *Geotrypetes seraphini occidentalis* Parker. LHT-HMS Coll. No. 4653, Tafo, Ghana, Africa. Total length of specimen, 354 mm; length of skull, 11.3 mm; width of skull, 7.7 mm.

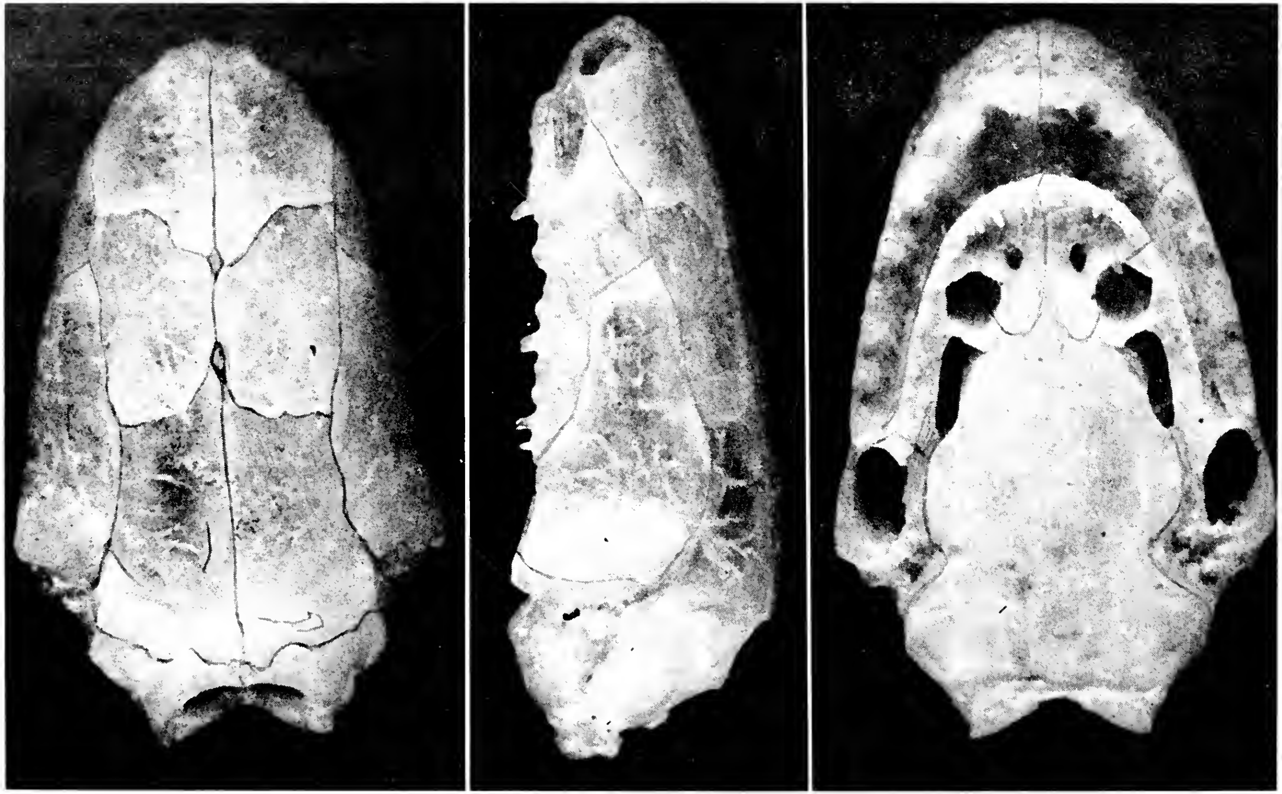

FIG. 42. *Herpele squalostoma* (Stutchbury). EHT-HMS Coll. No. 3412, Metet, Cameroons. Total length of specimen, 360 mm; length of skull, 10.7 mm; width of skull, 6.45 mm.

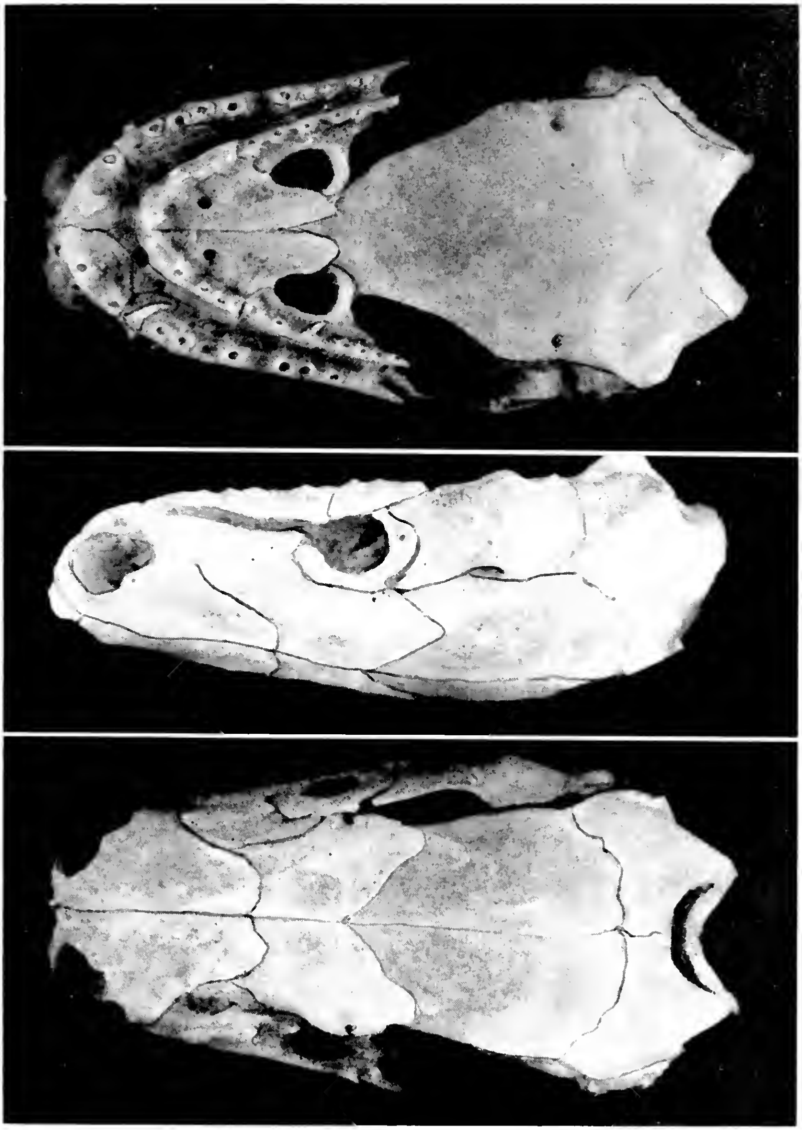

FIG. 43. *Uraeotyphlus oxyurus* (Duméril and Bibron). MCZ No. 9484, Taliparabamba Travancore, India. Length of skull, 7.8 mm; width of skull, 4.3± mm.

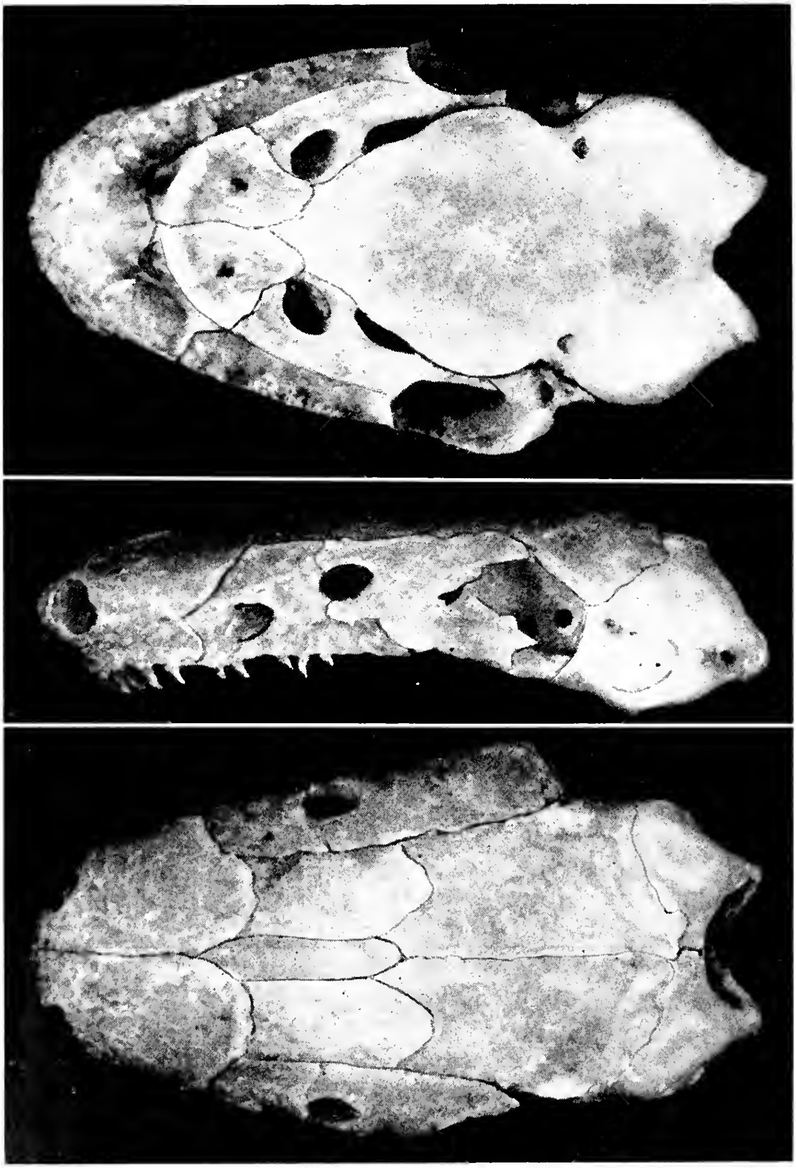

Fig. 44. *Schistometopum gregorii* (Boulenger). MCZ No. 20117, Lake Peccatoni, Kenya. Total length of specimen, 336 mm; length of skull, 10.4 mm; width of skull, 6.3 mm.

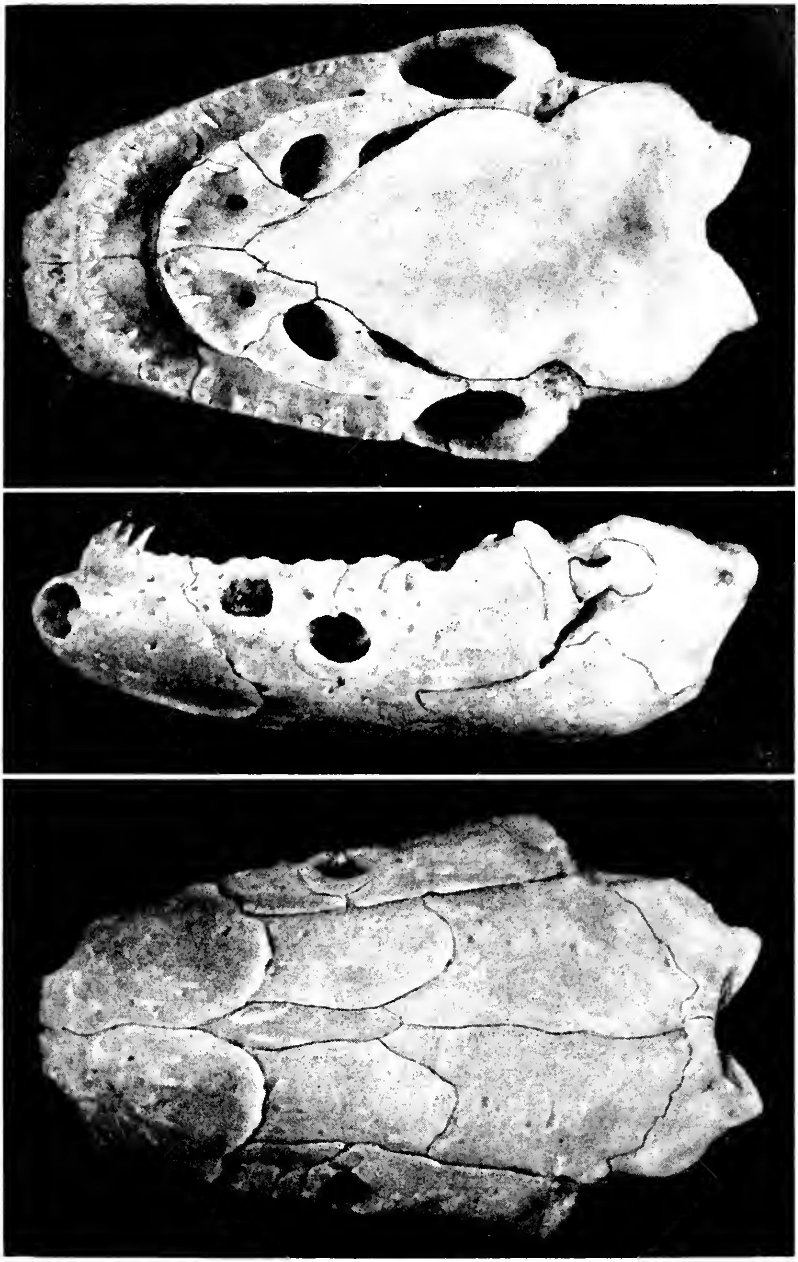

FIG. 45. *Schistomectopum gregorii* (Boulenger). MCZ No. 20146, Lake Peccatoni, Kenya. Total length of specimen, 356 mm; length of skull, 10.5 mm; width of skull, 6.7 mm.

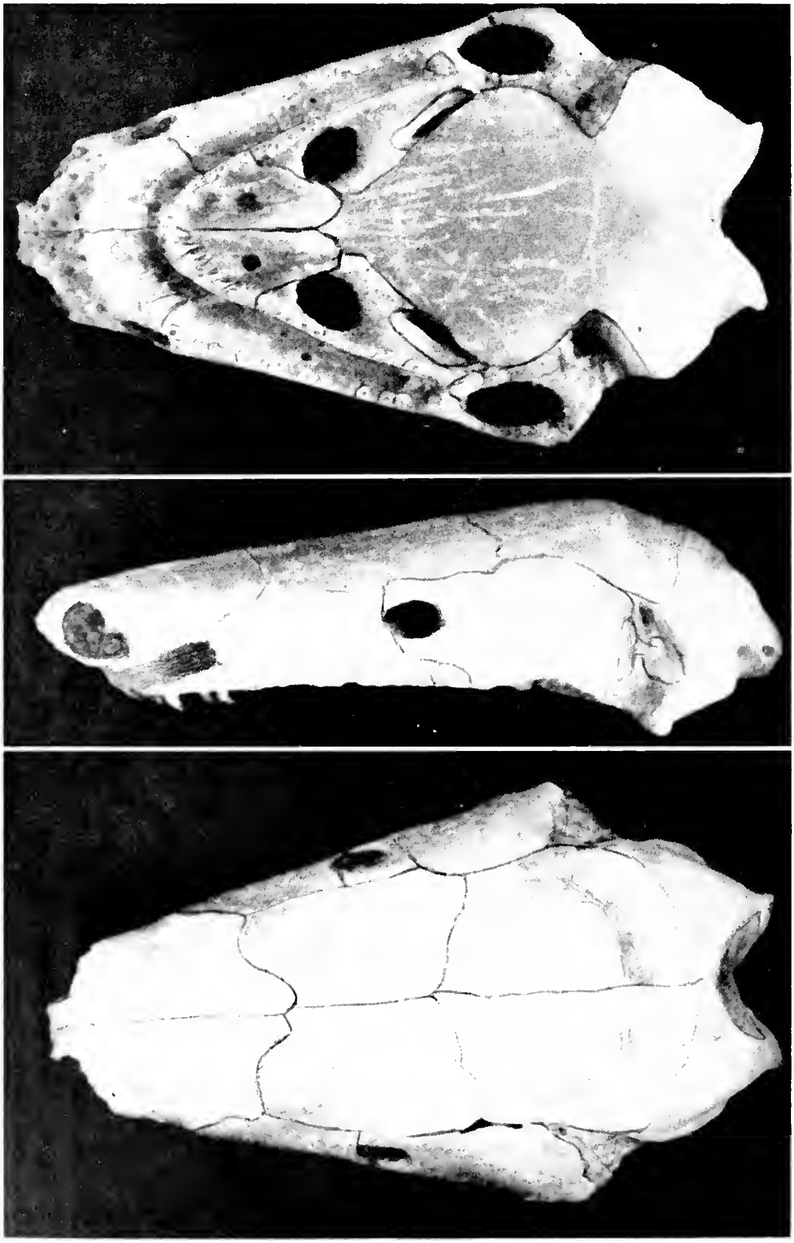

FIG. 46. *Hypogeophis rostratus rostratus* (Cuvier). MCZ No. 48935. St. Anne's Island, Mahé Coast, Seychelles Islands. Total length of specimen, 254 mm; length of skull, 8.6 mm; width of skull, 5.0 mm.

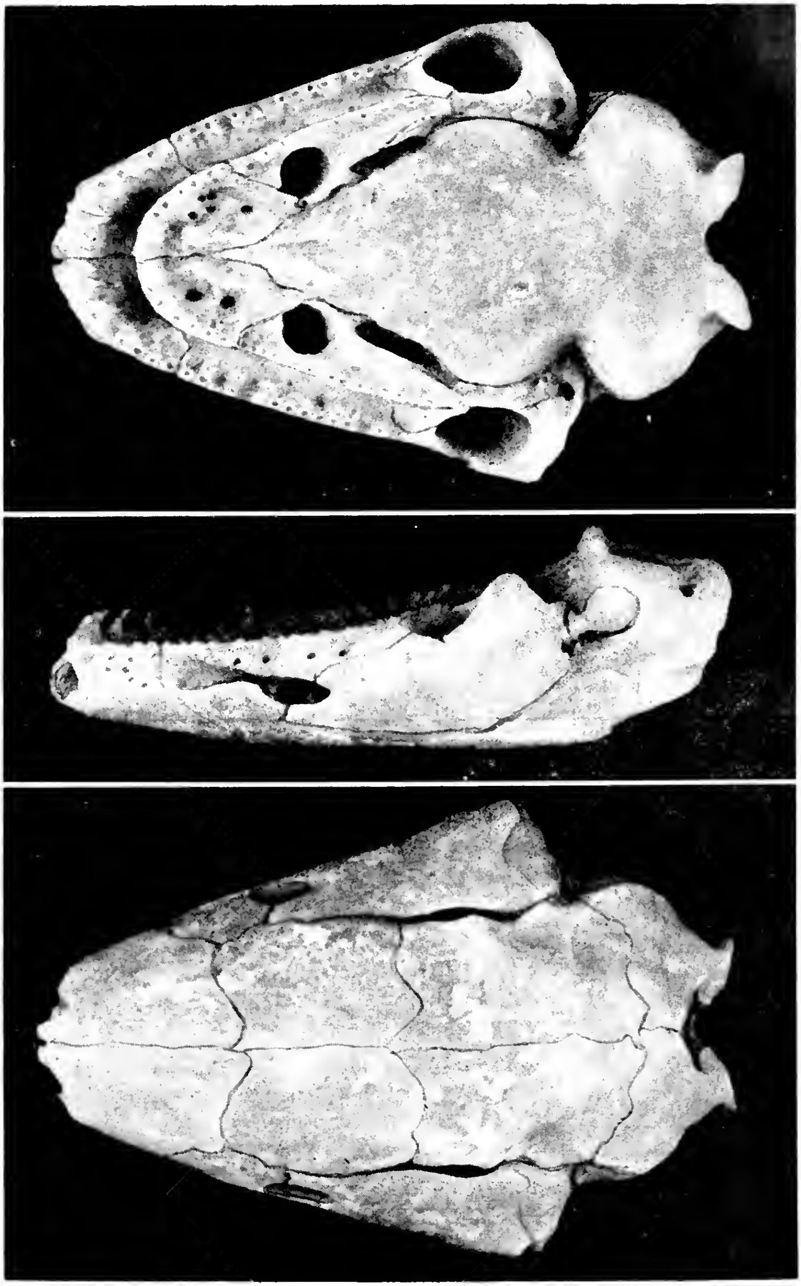

FIG. 47. *Grandisonia alternans* (Stejneger). EHT-HMS Coll. No. 4647, Mahé, Seychelles Islands. Total length of specimen, 216 mm; length of skull, 11.1 mm; width of skull, 7.0 mm.

FIG. 48. *Grandisonia sechellensis* (Boulenger). AMNH No. 23673, "Seychelles Islands." Total length of specimen, ? (broken); length of skull, 5.15 mm; width of skull, 2.8 mm.

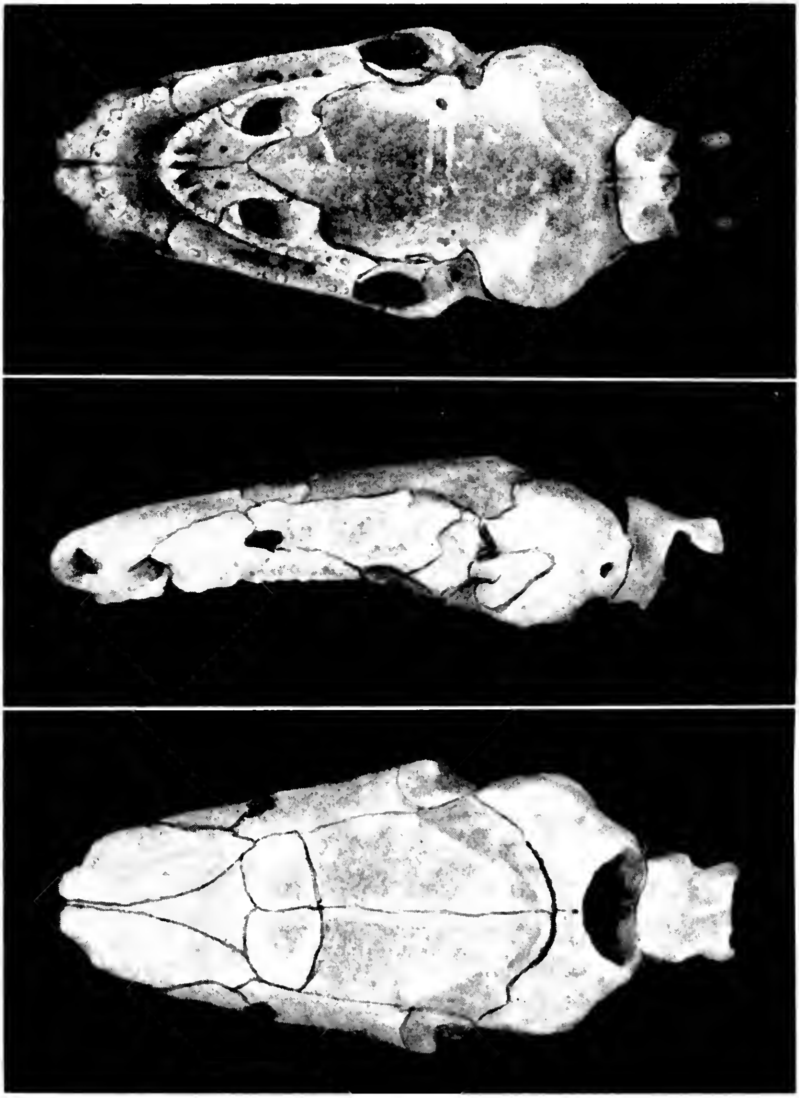

FIG. 49. *Idiocranium russeli* Parker. EHT-HMS Coll., No. 4687. Topotype. Cameroons. Total length of specimen, 102 mm; length of skull, 4.5 mm; width of skull, 2.2 mm.

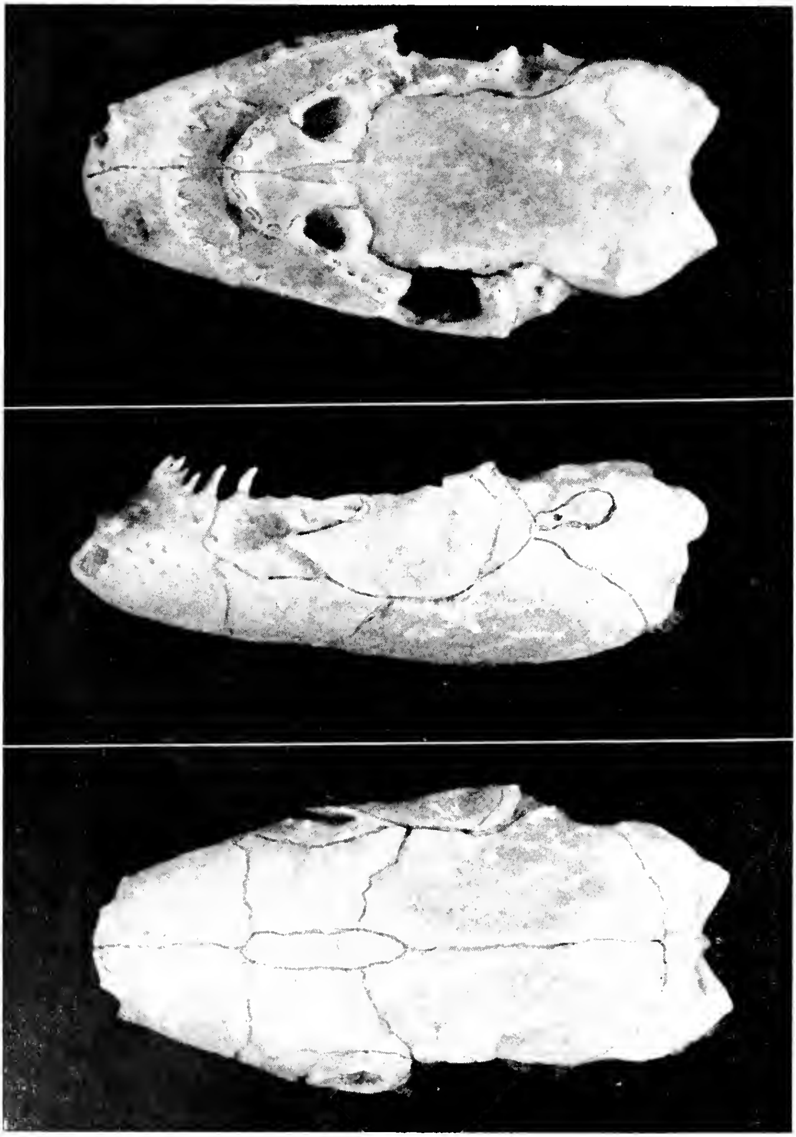

FIG. 50. *Boulengerula boulengeri* Tornier. MCZ No. 12309, Amani, Usumbara Mts., Tanganyika (Tanzania), Africa. Total length of specimen, 178 mm; length of skull, 4.7 mm; width of skull, 2.3 mm.

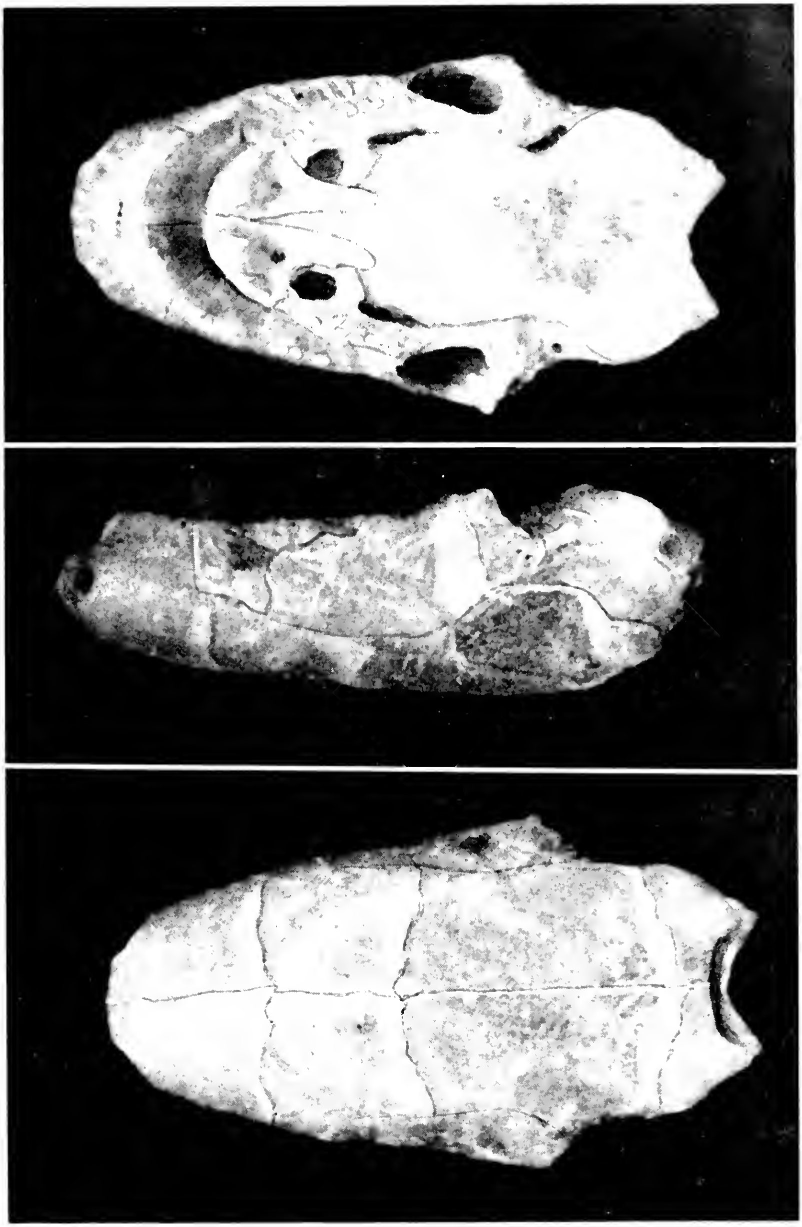

FIG. 51. *Afrocaecilia uluguruensis* (Barbour and Loveridge). EHT-HMS Coll. No. 4649, Vituri (2000 ft. elev.), Uluguru Mts., Tanganyika, Africa. Total length of specimen, 232 mm; length of skull, 5.8 mm; width of skull, 3.2 mm.

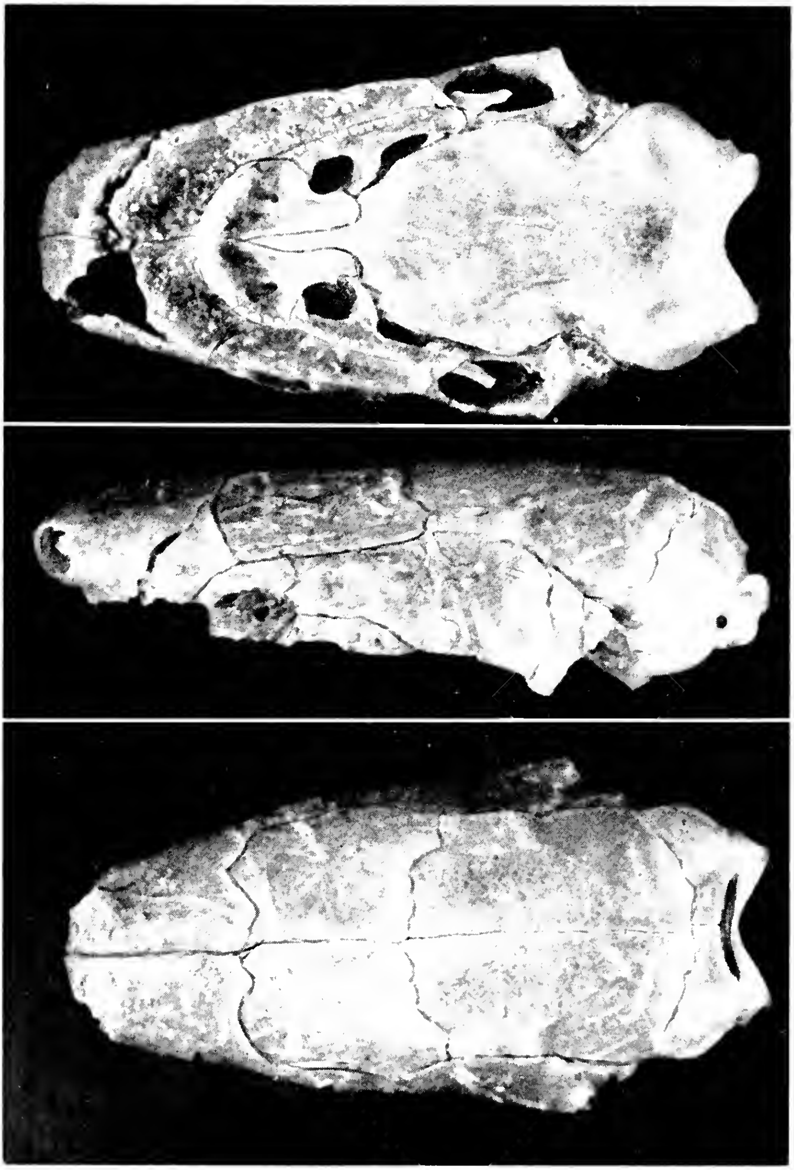

FIG. 52. *Afrocaecilia taitana* (Loveridge). MCZ No. 20021. Topotype. Teita Hills, Kenya. Total length of specimen, 234 mm; length of skull, 7.3 mm; width of skull, 3.6 mm.

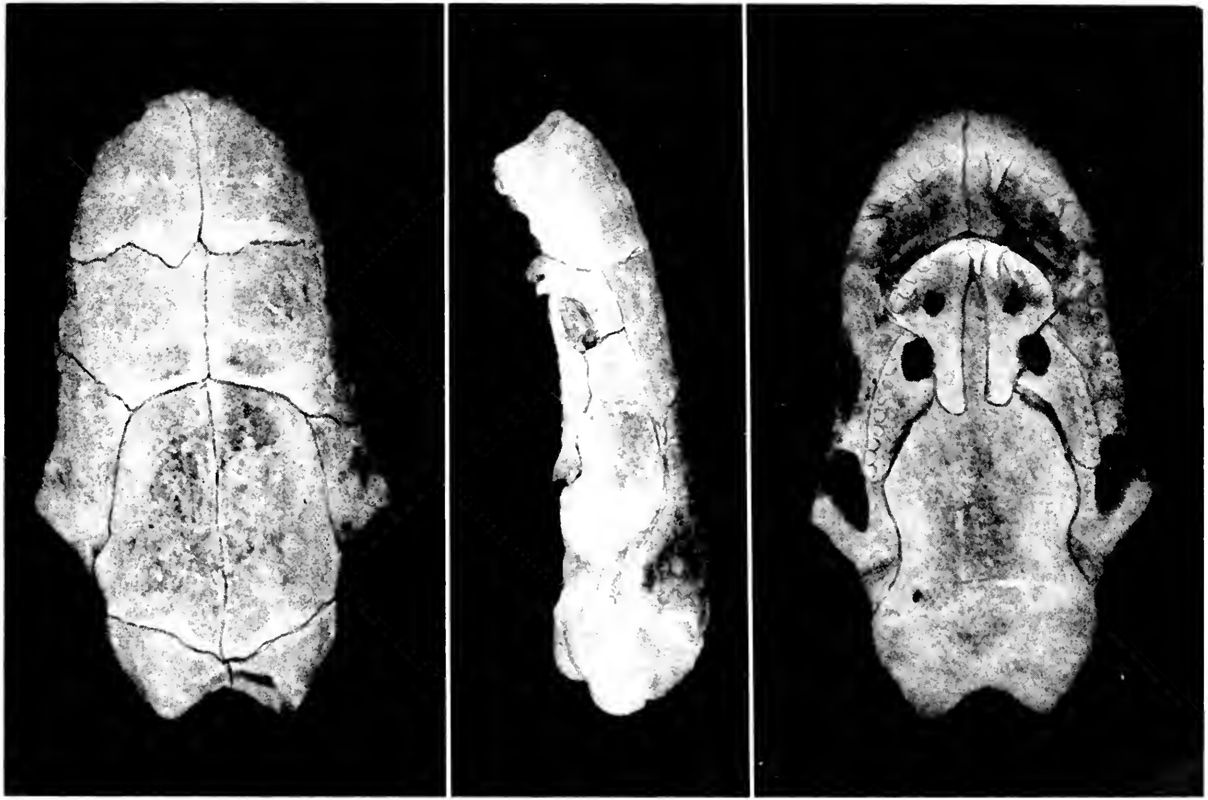

FIG. 53. *Afrocaecilia changamwensis* (Loveridge). EHT-HMS Coll. No. 4651. Changamwe, Kenya (192 ft. elev.). Total length of specimen, 234 mm; length of skull, 5.7 mm; width of skull, 3.25 mm.

FIG. 54. *Gegeneophis ramaswamii* Taylor. MCZ No. 29454, Tenmalai Forest, Kerala, Southern India. Total length of specimen, 263 mm; length of skull, 9.05 mm; width of skull, 4.95 mm.

FIG. 55. *Gegeneophis ramaswamii* Taylor. MCZ No. 29452, topotypic paratype, Tenmalai Forest, Kerala, Southern India. Total length of specimen, 305 mm; length of skull, 10.0 mm; width of skull, 6.0 mm.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVIII Pages 689-719 November 14, 1969 No. 16

Biology of the Bee Genus *Agapostemon* (Hymenoptera: Halictidae).[1,2]

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ABSTRACT

Insectary observations on life history, foraging, mating, sleeping and nesting behavior of *Agapostemon radiatus*, *A. splendens* and *A. texanus* are presented. The biology of the entire genus, insofar as known, is summarized. Lack of sociality and the presence of a single cell at the end of each of the long lateral branches of the main nest burrow support the conclusion that *Agapostemon* is more closely allied with a South and Central American group of genera than with the genera allied with either *Augochlora* or *Halictus*. Unlike many bees, none of the species of *Agapostemon* studied in the insectary lines its cells with materials other than those secreted by the bee constructing the cell and none constructs a spiraled cell closure. Field and insectary observations indicate that *A. radiatus* and *A. texanus* nest in loam and *A. splendens* nests in sand. Naive insectary-reared bees gather pollen without hesitation or ineptitude from flowers with tubular anthers, demonstrating that the complex and peculiar behavioral responses of bees to these flowers are innate and not learned. In the course of the study, a lighter and less bulky type of observation nest-box was developed for use in the insectary.

INTRODUCTION

Initiated as an adjunct to a revision of the genus *Agapostemon*, this study of the life history, nest architecture and nesting biology is in some respects preliminary. Nevertheless, biological information on this group of halictines is so scarce as to warrant such a study.

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[1] Contribution number 1414 from the Department of Entomology, University of Kansas, Lawrence, Kansas.

[2] This study was supported by National Science Foundation Grant GB 3151 to the University of Kansas (C. D. Michener, principal investigator).

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According to G. C. Eickwort (1969), the genera of American Halictinae can be placed in three groups: (1) the typically non-metallic group including *Halictus, Lasioglossum,* etc.; (2) the typically metallic group including *Augochlora, Augochlorella, Augochloropsis,* etc.; and (3) the typically metallic group including *Agapostemon, Paragapostemon, Pseudagapostemon,* etc. The nesting biology of representatives of the first two groups has been extensively studied both in the field and in the insectary by various authors (recent references are Batra, 1966; Ordway, 1966; Stockhammer, 1966). Biology of representatives of the *Agapostemon* group is poorly known. Detailed studies have been published on the nests of the South American *Pseudagapostemon* (Michener and Lange, 1958a) and *Ruizantheda* (Claude-Joseph, 1926) but despite its abundance, observations on the nesting biology of *Agapostemon* are few and sketchy.

Despite efforts to obtain data on field nests of *Agapostemon* from 1962 until 1967, I was able to find only a single nest, and it could not be excavated. Thus all my investigations on nesting biology were conducted in insectaries at the University of Kansas. Field observations on *Agapostemon* nesting made by others are compared with insectary findings. Certain published observations on "*Agapostemon splendens*" are, in large part, erroneous and are largely disregarded (see Appendix).

The species most common in the vicinity of Lawrence, Kansas are *Agapostemon texanus, A. radiatus* and *A. splendens.* All three were studied in the insectary, and the observations on nesting biology are based on 65 nests (28 *A. texanus,* 23 *A. radiatus* and 14 *A. splendens*).

ACKNOWLEDGMENTS

I am grateful to the following individuals for contributing both information and valuable suggestions used in this study: S. W. Batra, G. E. Bohart, G. C. Eickwort, K. Eickwort, W. B. Kerfoot, W. E. LaBerge, R. J. Lavigne, C. D. Michener, D. W. Ribble, W. P. Stephen and K. A. Stockhammer. Special thanks are extended to Dr. G. W. Byers and Dr. C. D. Michener for their helpful advice and careful editing of the manuscript, and to my wife, Guinnevere, for her aid in the preparation of the manuscript.

MATERIALS AND METHODS

The insectary in which the observations on nesting behavior were made consists of several small rooms with fluorescent lighting and air-conditioning. The rooms differ only slightly in size and intensity of illumination. The room used for most of the investigations of nesting behavior has been described by Batra (1964).

The fluorescent lights were operated by two electric timers. The majority of the lights were on one circuit and were turned on for 15 hours each day. The remaining lights were set to go on 30 minutes before the main lights and to remain on until 30 minutes after the main lights had gone off. The purpose of this two circuit system was to warn the bees of impending darkness, thus giving them an opportunity to enter their nests or find sleeping sites. A two step increase in light intensity used in the morning was probably unnecessary. The bees were kept on a 16 hour light regime in order to avoid the possibility of inducing ovarian diapause under "short day" conditions. More for the comfort of the investigator than for the bees, the air-conditioner was set to maintain a room temperature of about 82° F (27.7° C) during the summer months. At this temperature the relative humidity varied from 70-90%. During the fall and winter months the temperature dropped to about 70° F (21.1° C) and the relative humidity sometimes dropped as low as 50%.

In the field, female and male *Agapostemon* were captured at flowers. The bees were removed from the net with an aspirator consisting of copper tubing about 20 cm long and 7 mm in diameter. The copper tubing was attached to a piece of plastic (Tygon) tubing which was held in the mouth. The bees were sucked into the copper tubing but were prevented from entering the plastic tubing by a piece of fine mesh copper screening. They were retained in the copper tubing by covering the opening with a finger. The finger was removed as the tip of the aspirator was inserted through an X-shaped cut in the polyethylene lid of a "two pound" coffee can. A sharp puff expelled the bees from the aspirator and the X-shaped cut closed as the aspirator was withdrawn from the can. The polyethylene lid of the can was perforated for ventilation by melting numerous small holes with a heated wire. The can contained several crumpled sheets of damp paper toweling which provided the bees with a substrate to which they could cling, a cushion to prevent injury when they were expelled from the aspirator and a humid atmosphere to prevent dehydration. If the bees flew against the lid of the can or if the can became too warm, mortality rose rapidly to 100%. When the outside of the can was covered with aluminum foil to reflect heat and exclude light, the bees rested quietly on the toweling and could be carried in the field all morning in hot weather with little or no mortality.

In the insectary the bees were fed with both honey and fresh flowers. Honey was placed in the centers of plastic flowers and diluted with sufficient water (about one part water to two parts honey) to reduce its viscosity to the point where the bees could drink it. Excessive dilution reduces the osmotic pressure so much that yeasts and imperfect fungi become a problem. Even when sufficient flowers with nectaries are available, the bees frequently utilize the honey on the plastic flowers (Fig. 18). The availability of this honey prevented mass starvation on those occasions when fresh flowers were not available. It was found that female *Agapostemon* could be maintained on honey alone during late fall and winter when flowers were not available.

Flowers for feeding the bees were selected on the basis of the following criteria: abundance or obtainability, amount of pollen produced and longevity after being cut. In chronological order of their blooming, those used were: *Salix, Prunus, Malus, Cirsium, Amorpha, Ratibida, Silphium, Chamaecrista, Helianthus* and *Aster*. These flowers were also those most frequently visited by *Agapostemon* in the field. Other flowers frequently visited by *Agapostemon* (*Opuntia, Convolvulus,* and *Cucurbita*) wilt soon after cutting and were not utilized in the insectary.

In order to learn more about the behavior of *Agapostemon*, a large observation nest-box was constructed (Fig. 3). Modeled after those used by Batra (1964) in her study of *Lasioglossum*, its essentials were two sheets of plate glass (0.6 x 91.4 x 91.4 cm) separated by a 4 mm layer of soil, a wooden frame to hold the glass in place, a V-shaped trough of soil above the glass and black oilcloth over the glass to exclude light. As the weight of the layer of soil was sufficient to bow the glass outward, external braces were employed to maintain a constant distance of approximately 4 mm between the sheets of glass so that the burrowing bees would not be concealed by the soil. The main burrows, laterals, and cells of the *Agapostemon* species studied were all at least 4 mm wide so that the bees were visible through the glass. Only the cell entrances were slightly less than 4 mm wide and thus obscured by soil. The nest-box was none too large, for some individuals of *A. texanus*, *A. radiatus* and *A. splendens* dug all the way to the bottom. It was found that if damp soil were used in the initial construction of so large a nest-box, it would remain damp for at least six months, therefore no special means for replacing moisture were necessary. Desiccation of the top few centimeters of soil was prevented by lightly sprinkling the soil surface with water. It is easy to over-water this type of nest-box and pre-imaginal mortality is the result. While this large nest-box permitted simultaneous observation of as many as ten nests, it was satisfactory only for general observations inasmuch as the nests and their contents were inaccessible.

In order to permit access to larvae, two additional nest-boxes were constructed of sheets of transparent plexiglass 0.25 x 30 x 60 cm (Figs. 1-2). Holes were drilled in the sheets at about 10 cm intervals and the two sheets, spaced apart by washers, were bolted together. Wing nuts were used in order to facilitate subsequent dismantling. A single length of plastic (Tygon) tubing was forced between the two sheets along the sides and bottom to act as a seal. This technique proved very satisfactory and resulted in a nest-box which was unbreakable and lighter, stronger and more compact than glass nest-boxes. As the plexiglass nest-boxes required no bulky frame, they were easy to move and manipulate. The principal disadvantage of plexiglass is that it is easily scratched and has a greater tendency to bow outward, hence the necessity of bolting it at 10 cm intervals. The Tygon tubing seal on the sides and bottom of the nest-box is easily penetrated by a hypodermic needle, thus facilitating the addition of water or other fluids to the soil. In order to open the nest-box for the removal of larvae or to manipulate the contents of the nests, the nest-box is laid flat and the wing nuts removed. The top sheet of plexiglass is then removed, the soil not adhering to it as it does to glass. Later the plexiglass may be replaced and the nest-box set back in place with no damage to the contained nests.

Three soil-filled wooden boxes 30 x 45 x 30 cm were used in addition to the observation nest-boxes. These wooden nest-boxes accommodated nests of those bees not inhabiting the observation nest-boxes.

OBSERVATIONS

Seasonal Cycle

In the vicinity of Lawrence, Kansas, overwintering females of *Agapostemon texanus*, *A. radiatus* and *A. virescens* emerge from hibernation in April, when they are commonly found foraging on *Salix* spp. and *Prunus americana*. In May and early June, when *Salix* and *Prunus* have finished blooming and before most of the Compositae bloom, females of *Agapostemon* are rarely seen. In June flowers become abundant in the open areas and female *Agapostemon* are common on *Cirsium*. As the season progresses the number of females remains almost constant, but males become increasingly abundant. In June males are rarely found, but in late September they become extremely abundant and females become scarce.

Probably the three species of *Agapostemon* studied have only two generations per year in Kansas. One generation overwinters as fertilized females and, as evidenced by a few males collected in early April, about 0.1% of the males survive the winter. Overwintered females nest in April, and evidence from the insectary indicates that most of them die by mid-May. The summer generation begins to emerge in early June and consists almost entirely of females. These females begin nesting immediately and, judging by the appearance of numerous males in July and August, most of their offspring are males. The females which emerge in August could not be induced to nest in the insectary and are presumably the overwintering generation. These females may be distinguished from the summer generation by their unworn wings and mandibles and by their slender ovaries. These newly emerged females visit flowers for nectar and perhaps pollen (presumably to build fat reserves) and are fertilized by the very abundant males. Both males and females disappear after the first hard freeze (usually in late October). In the insectary these diapausing females spend most of their time in old burrows, emerging only occasionally to feed. Unlike nesting females, several of the diapausing females may crowd into a single burrow, or hibernaculum (Fig. 14).

This two-generation-per-year life cycle seems to be very efficient. Males are abundant only in the late summer and fall when there is a superabundance of food (*Silphium, Helianthus*, and other Compositae). The overwintering females are already fertilized when they emerge in the spring. They nest immediately and utilize the abundant and relatively localized pollen of fruit trees and willows in provisioning the cells which produce the summer generation. *Agapostemon* adults are essentially absent in May and early June, the period of heaviest rains, when the trees have finished blooming and before most of the pollen-rich Compositae bloom. Excluding wind pollinated species, the number of species of plants blooming in unwooded areas (*Agapostemon* is seldom found in woodlands) during May nearly doubles during June. In the aculeate Hymenoptera, males are normally produced from unfertilized eggs, and females from fertilized eggs. Presumably because their overwintered mothers were fertilized, the majority of *Agapostemon* emerging in June are females. The shortage of males in June means that many of the summer generation females lay unfertilized eggs, thus the majority of their offspring are males. The abundance of males in the late summer and fall ensures that most, if not all, of the females will be fertilized before hibernation.

NEST ORIENTATION

Individual species of *Agapostemon* are known to nest both in banks and in level ground, whereas many halictines nest in either one or the other. Nest entrances of the following species have been found in banks: *A. radiatus* (Rau, 1934), *A. nasutus* (Daly and Wille, *in* Sakagami and Michener, 1962; G. C. Eickwort, personal communication), *A. spendens* (Stevens, 1921) and *Agapostemon* sp. (probably *A. radiatus* or *A. texanus*, S. W. Batra, personal communication). Nest entrances of the following species have been found in horizontal or only slightly sloping surfaces: *A. radiatus* (LaBerge and Ribble, 1966; K. A. Stockhammer, personal communication), *A. splendens* (LaBerge and Ribble, 1966), *A. virescens* (Felt, 1928; W. E. LaBerge, D. H. Janzen and G. C. Eickwort, personal communications), *A. texanus* or *A. angelicus* (probably *A. angelicus*, personal observation), and *Agapostemon* sp. (W. B. Kerfoot, personal communication).

In the insectary *A. texanus, A. radiatus* and *A. splendens* were presented with horizontal soil surfaces. All three species readily entered these, but equally significant are nests (one of each species) which were entered through small apertures in vertical sides of the nest-boxes.

Sakagami and Michener (1962) included *A. splendens* in a list of "species whose nests are known only or principally from flat ground" but in the only reference cited (Stevens, 1921), the nest was in the side, or bank, of a sand "blowout," or wind-carved depression. In the light of my insectary observations and field observations of LaBerge and Ribble (1966) this species, together with *A. texanus* and *A. radiatus,* should be included in the list of species known to nest in both horizontal and vertical surfaces.

AGGREGATIVE TENDENCIES

There is some question as to whether the species of *Agapostemon* usually nest in aggregations or are usually solitary. Felt (1928) reported an aggregation of *A. virescens* (given as *Halictus virescens*) damaging a lawn in Catskill, New York: "Bare spots were reported here and there in the lawn and the bees were said to be burrowing more or less over its entire surface although there were areas where they were decidedly more abundant." W. P. Stephen (personal communication) has seen nesting aggregations of *A. virescens* in a lawn in Corvallis, Oregon and D. H. Janzen (personal communication) has found numerous nests of *A. virescens* in a field near Eugene, Oregon. Nesting aggregations of *A. nasutus* were found in Costa Rica by Daly and Wille (Sakagami and Michener, 1962) and by G. C. Eickwort (personal communication). Nests of *A. radiatus* may also be locally abundant, as Rau (1934) reported: "Dozens of these bees were at work burrowing vertically in a bank of very fine sand at Creve Coeur Lake, Mo., August 8, 1922." Stevens (1921) and LaBerge and Ribble (1966) reported finding nesting aggregations of *A. splendens.*

On the other hand, LaBerge and Ribble (1966) and K. A. Stockhammer (personal communication) have seen isolated nests of *A. radiatus*; K. A. Stockhammer, S. W. Batra and W. B. Kerfoot (personal communications) have seen isolated nests of *Agapostemon* spp., and I have seen an isolated nest of *A. texanus* or *A. angelicus* (probably *A. angelicus*). Insectary observations show that *A. texanus, A. radiatus* and *A. splendens* nest as readily in isolated containers as they do within a few centimeters of each other.

It appears that nests of *Agapostemon* species, unlike those of many of the halictines, may be either aggregated or solitary. The tendency to nest in aggregations seems to vary among the species. The species which are known only to nest in aggregations, *A. virescens* (W. E. LaBerge, personal communication) and *A. nasutus* (G. C. Eickwort, personal communication), are those in which numerous females often utilize a common burrow. Possibly the tendency of *A. virescens* and *A. nasutus* to nest in aggregations is linked to this mutual tolerance among females or possibly to some tendency for females to nest near their birthplace. The females of *A. texanus, A. radiatus* and *A. splendens* have not been seen to nest in natural aggregations as dense as those of *A. virescens* and *A. nasutus*, and in the insectary do not tolerate the presence of other females in their nests.

EDAPHIC PREFERENCES

Agapostemon splendens has been found nesting in the sand hills of North Dakota (Stevens, 1921) and in the sand hills of Nebraska (LaBerge and Ribble, 1966). In the insectary the bees were supplied with a choice of sand or loam in which to nest. All but one of the 22 nests of *A. splendens* were in sand, whereas *A. texanus* and *A. radiatus* always nested in the loam. Although the bees do exhibit edaphic preferences in the insectary, one must be careful in extrapolating from laboratory observations, as Rau (1934) and LaBerge and Ribble (1966) report *A. radiatus* nesting in sand.

The insectary and field observations on the edaphic preference of *A. splendens* are corroborated by its range and local distribution. This species is common only in the eastern three fifths of the United States and probably does not occur in very arid regions. Although I have seen several specimens from the arid Southwest, it is reasonable to assume either that they are mislabeled, were recent accidental introductions, or represent local populations in limited areas of moist sand. *A. splendens* is most common along the Gulf and Atlantic Coasts, the margins of the Great Lakes, and the sand hill regions of Kansas, Nebraska, the Dakotas, and Manitoba. In all of these regions sand is the principal soil type. Although I have collected *Agapostemon* extensively in the vicinity of Lawrence, Kansas, I have rarely seen *A. splendens* outside the sandy floodplain of the Kansas River.

The biological significance of the edaphic preference of *A. splendens* is obscure. From insectary observations it is apparent that excessive moisture and the resulting increase in the growth of fungi is correlated with, if not the cause of, high pre-imaginal mortality. As *A. splendens* nests in regions where the summer rains are frequently heavy, it is possible that a well drained soil (e.g., sand) with relatively few microorganisms would minimize the mortality of the pre-imaginal bees. Discounting the several specimens from the Southwest mentioned above, it is interesting that this species is not found in the desert or other areas of low precipitation even though sand is common in such regions.

NEST LOCATION

When first released in the insectary, the females of *A. texanus, A. splendens* and *A. radiatus* exhibit an "escape" reaction by flying up towards the lights and bumping against the transparent ceiling for about 15 minutes.

When the bees calm down, they begin visiting the flowers for nectar but not pollen. After some minutes of feeding and resting on flowers, some females begin what appears to be a "searching" or "investigating" flight. Almost all females captured in May exhibit this behavior but those captured later in the summer are increasingly refractory and by late August none of the females introduced into the insectary search for nest sites.

During this slow, wavering, "searching" flight the female flies about the room, 3-10 cm from the floor or walls. When flying above the floor she lands occasionally and walks about for a few seconds before resuming flight. When flying near the wall the bee always faces the wall, landing occasionally to investigate nail heads (which happened to be about the diameter of an *Agapostemon* burrow) or other dark spots on the straw-colored walls. This "searching" behavior is often interrupted by rests and visits to flowers for nectar.

The bees seem to be attracted to dark spots and shadows. When holes are poked in the soil of the nest-boxes with a pencil, the bees often enter the holes and begin nest construction. They also enter the nests of other bees and, unless ejected, begin further excavation.

Small stones and assorted plastic leaves were scattered on the surfaces of the soil in nest-boxes and, unless presented with the ready-made holes mentioned above, the bees made their nest entrances under the stones and leaves. When a stone is so embedded that the bees are unable to crawl under it, they begin digging at its margin. In the same manner, they dig at the intersection of the soil surface and the side of the nest-box. Although the bees initiate their nests under the stones and leaves, they do not abandon their nests if the stones or leaves are removed.

K. A. Stockhammer and S. W. Batra (personal communications) have seen *Agapostemon* nesting in the Lawrence area and every nest was either under a leaf or small stone, or at the intersection of vertical and horizontal soil surfaces. I have seen a nest of *A. texanus* or *A. angelicus* (probably the latter) concealed beneath a prostrate stem of *Opuntia* near Coaldale, Colorado. Neither Dr. Stockhammer, Dr. Batra nor I would have found the nests had we not been watching the returning females. Perhaps this common habit of secreting the nest entrance is one reason the nests of *Agapostemon* are seldom found. One can only speculate on the biological significance of this habit. It may conceal the nest from the eyes of parasites such as beeflies (Bombyliidae) or cuckoo wasps (Chrysididae). It may also serve to protect the nest entrance from rain.

NEST ARCHITECTURE

The nests of *Agapostemon* consist of a main burrow and laterals with cells. The long axis of the main burrow is normally perpendicular to the soil surface. The laterals normally slant slightly downward from the main burrow and are never at the end of the burrow. Cells are nearly horizontal, with the slightly constricted cell entrance slightly higher than the rear of the ellipsoidal cell. The undisturbed tumulus is a low symmetrical cratered cone of unconsolidated soil granules.

The nests of *A. nasutus* excavated by Daly and Wille and reported by Sakagami and Michener (1962) are unusual in that they had two end-to-end cells in most laterals with the older, terminal cell producing a female and the younger, sub-terminal cell producing a male.

Although the two end-to-end cells per lateral observed by Daly and Wille could not be confirmed by G. C. Eickwort and K. Eickwort (personal communication), it is interesting that the only other species with end-to-end cells in the laterals are South American halictines (*Pseudagapostemon divaricatus, P. perzonatus* and *Ruizantheda mutabilis*) closely allied to *Agapostemon* (cf. Sakagami and Michener, 1962). Field observations on *A. splendens* (Stevens, 1921) and *A. radiatus* (LaBerge and Ribble, 1966) as well as my own insectary observations on *A. texanus, A. radiatus* and *A. splendens* indicate that these species build only a single cell at the end of each lateral.

The deepest nests (1.5 m) and the longest laterals (30 cm) reported for *Agapostemon* are those of *A. splendens*, one of the largest species, excavated by Stevens (1921). In the insectary some females of *A. texanus, A. radiatus* and *A. splendens* dug all the way to the bottom of the largest nest-box (nearly 1 m in depth) where they constructed cells. While *A. splendens* females usually dug to the bottom of the nest-box, those of the smaller *A. texanus* and *A. radiatus* usually confined their excavations to depths of 20 to 60 cm.

The laterals of *A. texanus, A. radiatus* and *A. splendens* were narrower than the main burrow, as are the laterals of other halictines. The laterals of *A. texanus* and *A. radiatus* in nest-boxes were 5-15 cm long while those of *A. splendens* were from 8-20 cm long. K. A. Stockhammer (personal communication) has seen a nest of *A. radiatus* in which one of the cells was joined directly to the main burrow, although the others had laterals of various lengths. Although the laterals observed by me were filled after cell closure with soil taken from the sides of the main burrow, there were no obvious pits left in the walls. The largest number of cells and laterals constructed in a single nest was 14 in an insectary nest of *A. texanus*. The usual number of cells and laterals constructed by *A. texanus, A. radiatus* and *A. splendens* in the insectary was six to ten, with some females constructing as few as five.

NEST CONSTRUCTION

Aside from the edaphic preferences mentioned previously, no significant specific behavioral differences were noted in observations on *A. texanus, A. radiatus* and *A. splendens.* The nests of *A. splendens* were often deeper than those of *A. texanus* and *A. radiatus* (cf. NEST ARCHITECTURE) but this difference is proportional to the larger size of *A. splendens.* The following is a composite picture summarizing insectary observations on 28 nests of *A. texanus* (see DAILY ACTIVITIES for remarks on timing of the following activities).

After a female selects a site for her nest, she begins digging immediately. The forelegs and mandibles are used in loosening the soil, which is then passed beneath the body to the middle legs. Cupping the soil between the hind legs and the underside of the metasoma, she backs up about half her length and drops the soil. As she deepens the vertical burrow, the bee disappears beneath the tumulus (out of sight in about 15 minutes), making no attempt to keep the entrance clear of soil. Continued digging can only be inferred from dirt which is periodically pushed up from below until the bee appears between the glass or plastic sides of an observation nest. The tumulus is allowed to accumulate around the nest entrance and, if not disturbed or blown away, forms (on level ground) a symmetrical cratered cone 3-5 cm in diameter and 1-3 cm high. Perhaps because the bee does not remove the soil from the nest entrance until she leaves to forage, no turret is ever formed. The bee continues to deepen the nearly vertical burrow. If the bee encounters an obstacle, she deviates laterally until she can resume her downward course. At a depth of 10-40 cm the bee constructs her first lateral tunnel, which may or may not be at the bottom of the main burrow.

The lateral is slightly narrower than the vertical shaft and, while the bee can turn around in the main shaft and the cells by doubling back on herself in a forward somersault, she cannot turn around in a lateral. The soil excavated from the lateral is carried between the hind legs and the underside of the metasoma while the bee backs out of the lateral and up to the top of the main burrow, where she pushes it from the entrance. Sometimes the dirt gets away from her and drops to the bottom of the burrow. When this happens she often just leaves it until she is ready to deepen the burrow. The completed lateral slopes downward at about 10° (sometimes as much as 45°) from horizontal and is usually about 8 cm long, but may be as short as 5 cm or as long as 15 cm.

The female finishes the lateral by excavating an enlarged cavity, or cell, at its apex. The long axis of the cell is usually approximately continuous with that of the lateral and always slopes downwards at about 10-15°. Like the main burrow and the laterals, the cell cavity is excavated with the forelegs and mandibles. After excavation, the interior is tamped smooth by the pygidium. Although the bees were not seen to line the interior of their cells with dirt (Fig. 7) as do many other halictines, it is possible that I overlooked such activity. Next the female begins to "lick" the interior of the cell. In this process she turns around and around in the cell and, using the glossa as a brush, applies a liquid to the inside of the cell with short, rapid, forward motions of the partially extended mouthparts. As she licks and moves about the cell, she moves her hind legs with short, rapid, lateral motions, brushing the interior of the cells with the penicillus, a brush of hairs at the apex of each hind basitarsus. The liquid applied to the interior of the cell soaks into the soil and, in pale dry soil, may be seen as a dark zone around the cavity 1-2 mm thick (Fig. 5). After slightly over an hour of this licking and brushing, the female begins to tap the opened apex of the metasoma about the interior of the cell while wiping the interior of the cell with the penicilli. However, the hind legs are now moved so as to brush the interior of the cell with slower and more "deliberate" forward (rather than lateral) motions. I was not able to determine what, if anything, is added to the interior of the cell walls during this metasomal tapping. The tapping-brushing process lasts about two minutes before the bee leaves the cell to begin foraging. During most of the licking and metasomal tapping processes the antennae are usually flexed downward so as to touch the interior of the cell.

Completion of the new cell is followed by provisioning and oviposition. Immediately after the egg is deposited, the bee starts to leave the cell without pausing or turning around. Halting with the posterior half of her metasoma just inside the neck of the cell, the bee begins to rotate (about two seconds per revolution) about her long axis and wipes the open apex of her metasoma around the neck of the cell. After 10-20 revolutions the bee leaves the cell completely and begins scraping soil from the interior of the lateral adjacent to the cell with her forelegs and mandibles. This soil is passed rearward beneath the body by means of the middle and hind legs and is packed into the cell entrance with the pygidial region of the metasoma. Cell closure is completed in about two minutes. The female does not rotate in the lateral during cell closure and the resulting cell plug is unlike those of many bees in that it does not show a spiral construction pattern.

Having closed her cell, the bee leaves the lateral and proceeds up the main burrow for a few centimeters. She begins to dig at the walls of the shaft with her mandibles and forelegs, and the falling soil particles are caught between the wall and the hind legs and metasomal sterna. When she has accumulated a load of soil, she backs down the shaft and into the lateral. The load of soil is deposited at the rear of the lateral next to the closed cell, where it is tamped into place by the hind legs and pygidium. This procedure is continued for the 45-90 minutes necessary to completely fill the lateral.

Sometimes a load of soil is seemingly accidentally dropped to the bottom of the shaft. Attempts to retrieve the dropped soil are seldom successful, as the bee does not turn around and go after it head first. Instead, she backs down to the bottom of the shaft and tries to bring up the soil in the head-up position. This is usually unsuccessful because the soil particles catch on the wall of the shaft and roll out from between the metasomal sterna and the wall of the shaft, falling back to the bottom.

Some time after a lateral has been filled with soil, the bee begins to excavate a new lateral. This new lateral, with its terminal cell, may be either above or below the one just completed (Fig. 6). As the vertical shaft is periodically deepened, the bee is more likely to begin new laterals at progressively deeper levels, but this tendency is not pronounced. Although the length of laterals is quite variable, there is no apparent trend toward longer or shorter laterals as the nest is deepened. As each lateral is filled following cell closure, only one lateral and cell is open at a time.

The bees occasionally constructed abortive laterals. Sometimes the abandonment of a lateral was seemingly induced by observation, but in other instances abandonment of a lateral appeared to be spontaneous. Such laterals might be abandoned at any stage of construction, even after the terminal cell had been excavated. The aborted laterals were usually filled with soil in the same manner as completed laterals.

None of the females observed in the insectary was ever seen to begin a second nest unless (as was the case with two *A. radiatus* and one *A. texanus*) she was prevented from entering her original nest. Ordinarily a bee worked in her nest until her death. Most females died outside their nests, thus leaving them open; some (less than 20%) died inside their nests, which were sometimes plugged and sometimes open. Those females which died in their nests were soon covered by fungus but it was not determined whether the fungi were pathogens or saprophytes.

A female of *A. texanus* nesting in one of the wooden boxes was observed to close her nest in a unique manner. She emerged from the nest at 8:22 a.m. and began filling the burrow with earth from the tumulus. Biting at the earth with her mandibles, she raked it toward herself with the forelegs (used alternately) and, passing it backwards beneath her body, pushed the earth into her open burrow. The burrow was filled by 8:30 a.m. but the bee kept biting at the partially consolidated tumulus. She scattered the earth with lateral movements of her hind legs and forelegs. At 8:40 a.m., having leveled 80% of the tumulus and completely concealing the filled burrow, she flew away and never returned. As the bee was unmarked it is not known whether she started another nest. I can offer no explanation for this peculiar phenomenon, but as the entire sequence seemed well coordinated, such behavior may be normal under some circumstances.

PROVISIONING AND OVIPOSITION

As a bee does not have to go more than a few feet from her nest to find pollen and nectar in the insectary, the foraging trips may be short in duration. When pollen is abundant, the bee may gather a full load and return to the nest in as little as five minutes. The returning bee lands at the nest entrance, enters, and proceeds rapidly to the open cell. Entering the cell head first, she immediately turns around and removes the pollen load from the hind legs and metasomal sterna by rubbing the hind legs together and against the sterna while helping with the middle legs. The function of the large spatulate teeth on the posterior hind tibial spurs is unknown, but it is possible that they are used to help comb the pollen from the scopa. The bee takes slightly less than two minutes (1.75 minutes minimum observed) to enter her nest, deposit her pollen load in the cell, and leave on another foraging trip, providing she engages in no other activities.

The pollen from the first two or three loads is simply deposited as a dry, loose mass on the floor of the cell (Fig. 8). On the third or fourth foraging trip, the bee first takes nectar and, after spending some minutes at this, she collects a load of pollen and returns to the nest. After removing the pollen in the usual manner, the bee turns around once more and begins to mouth the pollen while scraping it together with her forelegs. Presumably nectar is regurgitated as the bee mouths the pollen mass. The mouthing and scraping together last 3-4 minutes, during which time the bee may turn around in the cell several times. Having thus moistened the pollen and shaped it into a crude loaf, the bee leaves on another foraging trip. Three or four more loads of pollen are added to the loaf. With each addition of pollen, the loaf is further worked with the mandibles and forelegs until it assumes the form of a slightly flattened ball. During the final stages of its formation, the ball is rolled back and forth in the cell while the bee works it constantly with mandibles and forelegs, all the while tapping the ball with the ventral apex of her metasoma and tapping rapidly on the floor of the cell with her flexed antennae.

Facing the cell entrance and grasping the finished pollen ball with hind tarsi only, the bee applies the apex of her metasoma to the rear of the upper half of the ball and sticks the apex of the emerging egg to the pollen. Then the hind legs are slowly straightened, pushing the bee forward until the anterior end of the egg drops on the pollen ball. In three observations of oviposition, extrusion of the egg took 30-35 seconds. The sausage-shaped egg rests on the upper rear of the pollen ball, supported only by the two ends of the egg (Fig. 9).

DAILY ACTIVITIES

The females of the three species of *Agapostemon* observed in the insectary spend the night in plugged burrows. When they are ready to forage in the morning, the plug is removed (I never saw this take place) and the bee usually spends several minutes with her head at the entrance before leaving the nest. In social halictines, resting with the head at the entrance is usually interpreted as "guarding" (Fig. 4). In *Agapostemon* (and perhaps in other solitary bees), it is doubtful that the female engages in nest defense while "guarding." If disturbed, the females of *Agapostemon* in the insectary would simply drop down their burrows. Even the slightest motion on my part was often sufficient to cause them to disappear for several minutes. If a slender blade of grass was poked down the burrow the female would sometimes try to push it out, but she would never come all the way up to the entrance.

The lights in the insectary were set to turn on at 7:00 and 7:30 a.m. Most bees begin foraging at about 9:00 a.m. and provisioning is usually completed by about noon, with oviposition taking place shortly thereafter. The cell is closed and the lateral filled with earth. The bee may then leave the nest to feed or she may remain inactive. Later in the afternoon she often begins deepening the burrow or constructing a lateral. The soil is ejected from the burrow and some of it plugs the entrance. During the afternoon or night a new lateral and cell may be constructed. Sometimes the new cell is not finished until mid-morning. This schedule is highly variable in the insectary and must be much more variable in the field where provisioning may be interrupted by cloudy or rainy weather and where flowers may be few and distant. In the insectary some individuals spend so much time "dawdling" on the flowers between provisioning trips that it takes as long as two days to provision a cell. During periods when pollen is scarce, provisioning might take as long as three days.

The reasons for abandoning a new lateral or cell are not always apparent, but if a bee in the process of deepening the vertical shaft or digging a lateral is exposed to too much light during observation, she soon becomes agitated and fills the excavations with soil. She may then leave the nest or simply cease all activity. As construction of a cell progresses, the bee becomes less and less sensitive to disturbance and once licking of the cell walls begins, she usually does not react to light by filling the cell with soil. After the first load of pollen is brought in, she can rarely be induced to abandon the cell. Unlike *Augochlora pura* (Stockhammer, 1966), cells of *Agapostemon* are usually not constructed late at night.

My impression is that the behavior of the female is controlled by some physiological factors (probably closely correlated with the maturation of oocytes) which are minimal following oviposition, cell closure and filling of the lateral. After she has filled the lateral, the actions of the female are unpredictable. She may peer out of the nest entrance for a while, work "half-heartedly" at deepening the burrow or simply rest in the burrow. As the hours pass she becomes more active, her activities seem increasingly "directed" toward completion of a new cell and she seems less susceptible to disturbances or distractions.

PRE-IMAGINAL DEVELOPMENT

The following is a summary of insectary observations on 38 cells of *A. texanus* during May and June. All but three of the 21 bees reaching maturity were males. Excessive watering of the nest-box was followed by fungal growth in 17 of the 38 cells. The temperature of the insectary fluctuated between 78-86° F (25.6-30.0° C). As this temperature is probably at least 20° F higher than the outside soil temperature, it is reasonable to assume that the development time of bees in the field is somewhat longer than that observed in the insectary.

It is very difficult to distinguish between an egg and a newly hatched larva, but it appears that the egg hatches about two days after oviposition. The larva eats constantly, except when moulting, and growth is very rapid. Within 4 to 5 days after hatching, the larva has consumed the entire pollen ball. Some of the large larvae were able to balance the partially eaten pollen mass on their abdominal venters (Fig. 10) until it was completely consumed. For about two days after the last pollen has been eaten, the mature larva turns around and around in its cell while making continuous feeding motions with the mandibles. Then it defecates on the floor and walls of the cell (Fig. 11), and lies on its back for 5-6 days as a prepupa (Fig. 12) before becoming a pupa (Fig. 13). The eyes turn pink on about the third day after pupation and turn dark brown after another three days. Next the body begins to darken in the head and mesosomal regions. The metasoma and appendages finally darken and, after approximately 16 days as a pupa, the bee moults for the last time. The adult remains in the cell for one or two days, presumably while the cuticle tans. Then it begins to dig its way out through the lateral and emerges from the nest one half to one day later. The elapsed time from oviposition to emergence from the nest was 32 ± 4 days for the males and about one day longer for the females, but this difference is not statistically significant.

ADULT LONGEVITY

In order to gauge the longevity of *Agapostemon* in the insectary, it was necessary to mark each bee in a distinctive manner. The most successful technique was to put small spots of various colors of quick drying model airplane paint on the mesonotum and metasomal terga. Mortality (about 30%) due to handling and painting was the most immediate disadvantage, but a second problem was the loss of the spots. On some individuals the paint spots remained for more than two months, on others they came off within 48 hours.

In the insectary the cause of death was often spiders concealed in the flowers, but frequently bees were accidentally crushed under foot or drowned in the honey on artificial flowers. The following represent the maximum number of days from marking to death (the total adult life span is undoubtedly somewhat longer): *A. texanus* ♂–22$^+$ days, ♀–67$^+$ days; *A. splendens* ♂–22$^+$ days, ♀–58$^+$ days; and *A. radiatus* ♀–63$^+$ days. The data listed above are based on observations of 70 marked bees (*A. texanus* 53; *A. radiatus* 12; *A. splendens* 5). Of course these data are for active bees, as overwintering females must live as long as 6 to 7 months.

MATING

Successful copulation was never observed in the insectary or in the field. However, attempts at copulation were seen repeatedly in the insectary and in the field. Once the males of *Agapostemon* leave their nests, they never return. Sleeping, eating, searching for mates and mating all take place on or about flowers. The mate-searching flight of the males is a very rapid oscillating flight which proceeds quickly from flower to flower. When the bee is flying in this manner it is difficult to follow with one's eye. The function of the oscillations can be only surmised, but it could serve to confuse predators which hunt by sight such as birds, robber flies and philanthine wasps, or it could serve to increase the depth perception of the searching male. The male approaches to 2-6 cm of the flowers but does not land except occasionally to take nectar or to rest. When the male locates a female on a flower, it ceases its oscillating flight and hovers about 5 cm from her. The male then situates itself so as to face the female from slightly above and either directly behind or directly in front, still at a distance of about 5 cm. After hovering for one half to one second in this position, the male darts at the female and grasps her with his legs. In each of my many observations of this action, the female successfully dislodged the male with her wings and occasionally her legs. Contact was never maintained for more than one second. The rejected male often repeats the hover-dart-grasp sequence two or three times before resuming its mate-searching flight. Apparently the males are poor at discriminating between the anterior and posterior aspects of the females, as they would approach from the front for almost half the attempts. It is obviously inefficient to be incorrectly oriented in 50% of the mating attempts, but consecutive attempts to mate with an unresponsive female would be advantageous if the previous rejection were a result of incorrect orientation of the male. All three of the species studied have females which are wholly green from above. However, in many of the species the abdomen of the female is conspicuously different in coloration from the head and thorax. It is possible that the differently colored abdomen in these species serves as a visual cue to the proper orientation of males. However, this may be offset by the similar appearance of males and females of these species.

Bohart (1950) describes mating in *Agapostemon femoratus* (given as *A. cockerelli*). Although the female of this species is wholly green when seen from above, the males approached the females from behind. Out of 32 attempts to mate with females of its own species, the males of *A. femoratus* were successful in 3 instances. Copulation lasted about 10 seconds before the male, which had clasped the female from above and slightly behind, was dislodged by the female. It seems probable that a female *Agapostemon* mates soon after emerging and never mates again. This could explain why mating of *Agapostemon* is so rarely observed.

Although males and females of *Agapostemon* frequently were seen to forage simultaneously on the same flower (Figs. 16-17) they never attempted copulation, and the usual interaction (if any) was for the female to drive off the male by lunging and biting as she would at another female.

The males of *Agapostemon* in the insectary will attempt to mate with nearly any insect on a flower. Bohart (1950) reported almost 30% of the mating attempts of *A. cockerelli* males were with females of *Halictus ligatus*, *H. farinosus*, *H. rubicundus* and *Lasioglossum* sp. In the flight chamber, males could even be induced to pounce on crude wood or clay models of females.

SLEEPING

Agapostemon are quite flexible in their sleeping habits. *A. angelicus* has been observed (Linsley, 1962) sleeping on the dried flower heads of a clump of *Heterotheca subaxillaris* (Compositae) in southeastern Arizona. Numerous males and occasional females were seen on these plants on 26 of 28 consecutive nights. According to Linsley, the females always slept alone but the males tolerated the presence of other male *A. angelicus* and as many as six males could be seen crowded onto one flower head. These males also tolerated the presence of wasps of the genus *Stenodynerus* (Hymenoptera; Vespidae). Grasping the plant with their legs, the male bees slept with their bodies extended, wings folded, and antennae held forward and pressed together or only slightly divergent.

On the morning of August 21, 1966, I observed males of *A. angelicus* sleeping on sunflowers (*Helianthus* sp.) in a pasture in eastern Colorado.

The bees slept on the tops of the flowers and in the morning both the bees and the flowers were covered with a heavy dew. As the morning was cold, the bees did not dry out and fly away until about 9:00 a.m. The sleeping posture was similar to that described by Linsley (1962).

A male of *Agapostemon femoratus* was observed by Hicks (1936) entering a hole in a sand bank at 5:00 p.m. When the tunnel was excavated, a female as well as the male was found in the hole. As no cells were found, the burrow was probably not being used as a nest.

On June 7, 1916, in Manatí, Puerto Rico, G. N. Wolcott (1948) observed, "A cluster of twenty or thirty of these bees [males of *A. viequesensis* given as *A. portoricensis*] was noted on a few grapefruit leaves." Although he makes no mention of the time of day, this may have been a sleeping aggregation.

Insectary observations showed that males of *A. texanus, A. radiatus* and *A. splendens* sleep most frequently on flowers. They are usually found on top of the flowers, although they can often be found on the underside. They occasionally sleep in abandoned burrows, but are chased out of any burrow containing a female. A block of wood about 20 cm long, 5 cm wide and 1.5 cm thick was hung from the ceiling of the insectary about 1.75 m from the floor. Males frequently slept in the 5 mm holes which had been drilled through the block. Females normally spent the night in their nests, but sometimes spent the night beneath a flower head or clinging to the ceiling of the insectary. Both males and females of the species studied slept with the body extended and never were seen to hang by the mandibles as do numerous Hymenoptera, including the *Nomada* which sometimes shared the insectary with *Agapostemon.*

FORAGING

In my experience (corroborated by the flower records from pinned specimens and the literature), the species of *Agapostemon* are polylectic and may be found at almost any time of day at almost any type of flower physically available to them (realizing their morphological limitation). Of course under a particular set of conditions the bees often prefer one flower species to another, but as conditions change (*e.g.*, as different flowers appear) these preferences also change. In the insectary a female sometimes gathers pollen from more than one flower species during a single foraging trip. On any one trip a bee more commonly gathers pollen from flowers similar in color and shape *(e.g., Silphium* and *Grindelia)* than from very dissimilar species *(e.g., Silphium* and *Cirsium).* Proximity of the blossoms is an additional factor, as the bees have a tendency to work with a clump of flowers which are, more often than not, conspecific. In any event, only an intensive behavioral study would yield useful information on the flower preferences or constancy of these bees.

A label which simply states, "on *Helianthus annuus*" is not very informative. If the bee were a male, it might have been taking nectar, looking for a mate, sleeping, or merely resting. If it were a female, it may have been taking nectar for its own use or for its offspring, collecting pollen, mating, resting, or sleeping. Certainly these are widely divergent activities, if resting and sleeping can be so classified, and should not be lumped under the headings "Flower Records" or "Flower Preferences." Although there are reliable reports on the activities of *Agapostemon* at flowers, they are written primarily from the viewpoint of floral biology.

Both males and females of *Agapostemon* can be found obtaining nectar or pollen at flowers at any time during the daylight hours. In Kansas, the best time to collect *Agapostemon* is from about 9:00 to noon, CST. While the abundance of females on flowers decreases rapidly in the afternoon, males remain at flowers throughout the day. Insectary observations show that provisioning females usually seal themselves in their nests in the afternoon, having finished provisioning a cell in the morning. However, females not provisioning nests spend most of their time during the day on or about flowers.

It is obvious that the females are able to adapt their pollen collecting behavior to coincide with the availability of pollen, and the males to the availability of females. *Agapostemon angelicus* has been reported (Linsley and Hurd, 1959) gathering pollen from *Mentzelia pumila,* which flowers in late afternoon, as late as 5:40 p.m. (sunset). The same species has also been reported (Linsley, 1960) collecting pollen from the matinal flowering *Cucurbita foetidissima* at 5:35 a.m. when the air temperature was 52-54° F (11.1-12.2° C) and a heavy overcast was threatening rain. In the same paper, Linsley reports *A. melliventris* collecting pollen from *Datura* sp. at 4:56 a.m., when it was so dark that a flashlight was used to examine the flowers.

The versatility of foraging *Agapostemon* is further demonstrated by *A. texanus, A. radiatus* and *A. splendens,* which I have seen collecting pollen from the horse nettle, *Solanum carolinense,* and the buffalo burr, *S. rostratum* (Solanaceae), as well as the showy partridge pea, *Chamaecrista fasciculata* (Cassiaceae), in Lawrence, Kansas. On these flowers the female bee grasps the cluster of tubular anthers with her legs and covers the apex of the anthers with the ventral surface of the thorax. Her head and abdomen flexed and wings folded, she grasps one of the pollen tubes with her mandibles (Fig. 15) and vibrates her thorax in several rapid bursts about 1/2 second in duration so as to emit a series of audible buzzes. The bee then transfers the pollen from the underside of her thorax to her hind legs.

She flies to another flower and repeats the performance. Michener (1962) and Wille (1963) have observed this buzzing behavior on tropical species of *Solanum* and *Cassia*. A wide variety of bees, including *Agapostemon*, were reported to exhibit this behavior. Michener speculated that grasping the pollen tubes with the mandibles serves to loosen the pollen within the tubes. While this may be true, insectary observations lead me to believe that the bees grasp one of the tubes during the "buzz" primarily to prevent being dislodged by their own vibration. Despite their efforts to cling to their precarious perch atop the anthers, the bees often slip and fall from the flower during "buzzing." No attempts to chew at the anthers were observed and the bees only grasp with the mandibles at the time of "buzzing." I concur with Michener in his contention that this "buzzing" behavior is inherited and not learned because inexperienced bees reared in the insectary went to flowers of *Solanum carolinense, S. rostratum* and *Chamaecrista fasciculata* and began "buzzing" without hesitation.

On most flowers the bees rake pollen from the anthers with the forelegs, the mandibles and possibly the labrum. Pollen accumulates in the thick brush of hairs on the flattened fore-basitarsus. The foreleg is swung to the rear and clamped between the base of the femur and the apex of the tibia of the middle leg. There is a longitudinal row of stout bristles on the distal half of the ventral surface of the middle tibia and a similar row on the basal half of the ventral surface of the middle femur. The bristles of these combs are directed slightly rearward. Pollen is removed from the basitarsal brush of the foreleg as it is drawn forward through the opposed combs of the flexed middle leg. The flexed middle leg simultaneously moves rearward and presses the mass of pollen into the scopa on the hind femur. This passage of pollen from foreleg to hind leg is so rapid as to be very difficult to observe. However, the positions of the legs can be seen in my high speed (1/1000 sec.) color photographs. Pollen is passed by the legs on one side at a time, presumably because simultaneous transfer by both right and left legs would leave the bee in the awkward position of having to stand on only two legs. As pollen accumulates on the hind legs, the bee pauses to press the hind legs and ventral surface of her abdomen together, thus packing the pollen. When pollen is abundant, significant amounts are carried on an abdominal scopa. It is possible that pollen is transferred to the abdominal scopa during the packing process. The ventral surface of the hind tibia is concave and glabrous, but with stiff bristles laterally. When the hind leg is flexed, the ventral surface of the hind tibia compacts and helps hold the pollen in the femoral scopa.

Owing to their long flight season and to their relative abundance, the species of *Agapostemon* are doubtless among our more important pollinators of native plants. They can also play an important role in the pollination of crops. Linsley (1946) and Linsley and MacSwain (1947) report that the individuals of *A. melliventris* are more effective pollinators of alfalfa than are individual honeybees. Bohart (1957) shows that females of *A. femoratus* (listed as *A. cockerelli*) trip 6-10 flowers per minute, those of *A. virescens*, 8-10 flowers per minute, and males of both species 1-5 flowers per minute. The investigations of LaBerge, Isakson and Kehr (1965) indicate that *A. texanus* is not an effective pollinator of alfalfa in screen cubicles 3 feet on a side. Although they neglect to mention the sex of the bees used, I assume they were females. If the bees were not nesting in the cages, it is unlikely they would collect pollen. Thus the results of this study seem irrelevant to what one might expect of uncaged bees.

From my own observations and the observations of others, *Agapostemon* ranks close behind *Apis*, *Bombus*, *Peponapis* and *Xenoglossa* in abundance on the flowers of Cucurbitaceae. In the desert Southwest, Linsley (1960) reports *A. melliventris* and *A. angelicus* as common on the flowers of *Cucurbita*. In Kansas *A. splendens*, *A. texanus* and *A. radiatus* are common on *Cucurbita* and, judging by the collections of squash pollinators from the University of California at Berkeley, *A. nasutus* is the species of *Agapostemon* most abundant on tropical squashes. While this information indicates the importance of *Agapostemon* as a pollinator, it should not be construed as host preference.

As Batra (1966) was able to induce *Lasioglossum zephyrum* to accept frozen pollen, attempts were made to induce *Agapostemon* to do likewise. Frozen pollen from *Alnus* (the same sample used by Batra) and *Malus* was offered to the bees on a wide variety of substrates including various plastic flowers and living flowers. Although efforts were made to present the pollen as naturally as possible, all was to no avail. The bees would walk through the pollen to obtain honey or nectar but if any pollen adhered to them, it was removed by grooming. Although *Lasioglossum* would collect even pollen spilled on the floor, *Agapostemon texanus*, *A. radiatus* and *A. splendens* ignored frozen pollen. If *Agapostemon* could have been induced to accept frozen pollen, it would have been possible to maintain them in the insectary throughout the year.

In the insectary foraging females (never males) were frequently seen "evaporating" nectar (Figs. 19-21). A bee engaged in this process rests on her middle and hind legs with her forelegs drawn up under the thorax. A droplet of nectar is regurgitated, and about once each second the mandibles are opened, the labrum and proboscis extended, and then the labrum and proboscis retracted and the mandibles closed. The droplet of nectar is extended on the base of the extended proboscis and when the proboscis is retracted into the proboscidial fossa the nectar clings to the underside of the genal area. Rhythmic movement of the mouthparts lasts for 5-15 minutes. Undoubtedly some water in the nectar evaporates in the process, and it seems reasonable to assume that the function of this activity is to concentrate or otherwise condition the nectar prior to adding it to the provisions in the cell.

Predators and Parasites*

No attempt was made to compile a list of organisms preying on species of *Agapostemon*. To do so would be difficult and the resulting list would undoubtedly be very incomplete and of dubious significance. It is apparent from the literature and from my observations that the following families of arthropods are important enemies of *Agapostemon*: crab spiders (Araneida; Thomisidae), ambush bugs (Hemiptera; Phymatidae), philanthine wasps (Hymenoptera; Sphecidae) and robber flies (Diptera; Asilidae). Owing to their cryptic coloration, crab spiders (most commonly *Misumenoides formosipes*) and ambush bugs were sometimes overlooked on cut flowers supplied to the insectary, and a single spider would often kill several bees before it was discovered.

The absence of published records of nest parasites of *Agapostemon* reflects the paucity of field data on the nests of these bees. The only positive evidence of parasitism is the single coarctate larva of a blister beetle (Coleoptera; Meloidae) recovered from a cell of *A. texanus* in the insectary. As the phoretic larvae of blister beetles were found on numerous pinned specimens of *Agapostemon*, it seems reasonable to assume that the bees are commonly parasitized by these beetles. The phoretic larvae of rhipiphorid beetles, also found on the pinned bees, may parasitize *Agapostemon*. Conspicuous by their absence were the Strepsiptera, common parasites of other halictid and andrenid bees. I examined about 50,000 specimens of *Agapostemon* without seeing a single strepsipteran. Mites are commonly found on both sexes of *Agapostemon* but identification was not attempted. Many of the mites are phoretic hypopi and are often symmetrically arranged in particular positions on the bees. It is probable that the life cycle of some of the mites is closely linked with that of the bees. Mites were not observed on the bees or in their nests in the insectary.

Probable parasites of *Agapostemon* are bee flies (Diptera; Bombyliidae), velvet ants (Hymenoptera; Mutillidae), and parasitic bees in the genera *Sphecodes* (Hymenoptera; Halictidae) and *Nomada* (Hymenoptera; Anthophoridae). Linsley, MacSwain and Smith (1954) report a female *Nomada* around a burrow of *A. texanus* and I have observed large numbers of *Agapostemon* and *Nomada* flying together. In late July, 1967, about 50 *Nomada* sp. were released in the insectary with nesting *Agapostemon*. Although these *Nomada* flew about, took nectar from, and mated on the

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* Parasite is used here in a broad sense to include inquilines and parasitoids.

flowers, they were never seen to search for or exhibit interest in the *Agapostemon* nests.

DISCUSSION

The behavior of the three species of *Agapostemon* observed in the insectary does not differ significantly from that described for *Lasioglossum zephyrum* (Batra, 1964), *Augochlorella* spp. (Ordway, 1966), and *Augochlora pura* (Stockhammer, 1966), excepting those activities directly associated with differences in nest architecture and with a lack of sociality. Unlike the smaller Halictinae (including those mentioned above), females of *Agapostemon* are not known to lick objects when away from their nests.

As yet there is no evidence of true sociality, with the concomitant castes and division of labor in the genus *Agapostemon* and its allies. Some of the species of *Agapostemon (e.g., A. texanus)* are known to be solitary while other species *(e.g., A. virescens)* probably live in communal nests, in which two or more egg-laying females occupy a single burrow without cooperating in construction of laterals or provisioning of cells. Species of *Pseudagapostemon* (Michener and Lange, 1958a) and *Ruizantheda* (*Halictus mutabilis*; Claude-Joseph, 1926), closely related to *Agapostemon*, live in communal nests but do not exhibit sociality. The augochlorine and *Halictus-Lasioglossum* groups of genera contain both solitary and social species but, in contrast to *Agapostemon* and its relatives, are not known to occupy communal nests. As so few species have been investigated, it seems premature to conclude that sociality does not occur in members of the genus *Agapostemon* and its allies.

The nests of *Agapostemon* and its relatives, *Pseudagapostemon*, *Habralictus* and *Ruizantheda*, are easily distinguished from those of most other Halictinae by their relatively long laterals (1-30 cm). Excluding the members of the *Agapostemon* group of genera, the only species with relatively long laterals are *Lasioglossum leucozonum* and several other species of *Lasioglossum*.* The three nearctic species of *Agapostemon* whose nesting biology has been investigated excavate a single cell at the end of each lateral, but it seems that the neotropical *A. nasutus* sometimes constructs a pair of contiguous cells at the end of the laterals. This habit of building two or more cells end-to-end in the laterals is known in the Halictinae only for *Agapostemon* and its allies. Conversely, the *Agapostemon* group of genera are not known to build the nests without laterals or with the cell

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* Nests of *Caenaugochlora curticeps* described by Michener and Lange (1958b) also had relatively long (1-4 cm) laterals. The authors noted that the nests were very different from those of other *Caenaugochlora* species and very similar to those of *Pseudagapostemon* and *Habralictus*. As suggested by Michener and Lange, *Caenaugochlora curticeps* probably belongs in another genus. On the basis of its nest architecture, *C. curticeps* is closely related to *Agapostemon* and should not be placed with the augochlorine genera.

clusters common to both the augochlorine and *Halictus-Lasioglossum* groups. *Agapostemon* and its relatives retain the usual apoid habit of constructing a cell, provisioning it, laying an egg, and closing it before going on to start the next cell. In the augochlorine and the *Halictus-Lasioglossum* groups this sequence often breaks down, several cells being in various stages of construction and provisioning at the same time even in nests inhabited by only a single adult female. None of the species in the *Agapostemon* group are known to construct a turret at the nest entrance, unlike many species in the augochlorine and *Halictus-Lasioglossum* groups. Many of the Halictinae *(e.g., Halictus farinosus)* have a strong tendency to excavate each new cell below the preceding cell, but in the insectary about 40% of the new cells of *Agapostemon* were excavated above older cells.

APPENDIX

The cells and larvae described as *A. splendens* by LaBerge and Ribble (1966) were so anomalous as to lead me to conclude that they were not made by *Agapostemon splendens* or any other member of the Halictinae.

The cells were vertical and spaced at intervals along a single lateral. This type of cell arrangement is unknown in the Halictinae but is common in the North American *Nomia* of the subgenera *Epinomia* and *Dieunomia* (Cross and Bohart, 1960). Furthermore, the described cells are very elongate, unlike the oval cells of *Agapostemon* constructed in the insectary.

The authors comment on the larvae found in the vertical cells, stating that: "The morphology of the larvae is generally similar to that of other halictid bees as described by Michener (1953). However, the strongly bidentate mandibles of *splendens* seem unique." In point of fact, strongly bidentate mandibles occur in the larvae of some of the Halictidae (Michener, 1953) and therein lies the explanation for this apparently anomalous nest. Although none of the Halictinae have bidentate mandibles in the larvae, those of the subfamily Nomiinae are characterized by strongly bidentate mandibles.

Only six species of *Nomia* are known from Nebraska: *Nomia nortoni*, *N. universitatis*, *N. apacha*, *N. heteropoda*, *N. nevadensis* and *N. triangulifera*. The cells were not made by *N. heteropoda* or *N. nevadensis* because they were too small for the former and too large for the latter. *Nomia nortoni* makes a cluster of cells rather than a linear series (Ribble, 1965) and nothing is known of the biology of the uncommon *N. apacha* and *N. universitatis*. The species most likely to have constructed the cells is *Nomia triangulifera*, a very common Nebraskan species which nests in sandy areas like that described by LaBerge and Ribble. The dimensions of the cells of *N. triangulifera* given by Cross and Bohart in 1960 (cell width 8.5 mm, cell length 20-22 mm, and cell neck 8-10 mm) are nearly identical with those described by LaBerge and Ribble (cell width 9 mm, cell length 20 mm, and cell neck 10 mm).

Seemingly contradictory is the fact that *Nomia triangulifera* does not begin to nest until the second week of August, whereas LaBerge and Ribble excavated the nests between the ninth and fifteenth of June. The "larva" figured by LaBerge and Ribble is "7" shaped and has very prominent tubercles. Both the angular appearance and the tubercles are characteristic of prepupae, feeding larvae being "C" shaped and only slightly tuberculate. The "pollen" in the cells presumably must have been the undigested pollen shells voided by the defecating larva. Feces of *N. triangulifera* are deposited on the bottom of the cell and could be confused with pollen. The last cell in the series of four was open and contained pollen but no larva. It is possible that the female was in the process of provisioning this cell when she died. That she expired prematurely is also indicated by the small number (4) of cells—*N. triangulifera* normally making 6-13 cells along a lateral.

The fact remains that *A. splendens* females were found in some of the burrows. As it was early in the season, it is possible that many of these females were still excavating their vertical shafts but had not yet begun to excavate laterals and cells. This interpretation is supported by the fact that LaBerge and Ribble reported finding only six cells, although 22 nests were excavated. Two of the six cells were not visibly connected with a vertical shaft but were assumed to have been constructed by the same bee which had constructed the main burrow some 3 cm distant. As these cells contained the only "mature larvae" recovered, one must conclude that the "mature larva" of their figures 3-8 was not found in the nest illustrated in Figure 1.

Prepupae of *N. triangulifera* were compared with the immatures of "*A. splendens*" collected by LaBerge and Ribble (kindly lent by LaBerge) and were found to be indistinguishable.

Insectary observations of *Agapostemon* show that the females and sometimes the males will take up residence in any unoccupied hole or burrow. This may explain their presence in what seem to be burrows of *Nomia triangulifera.*

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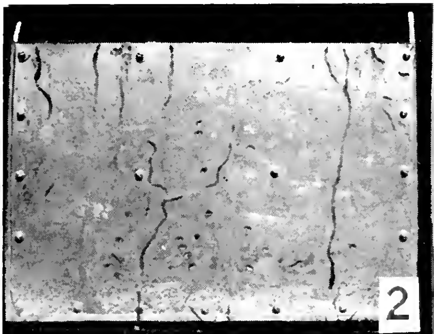
FIG. 1. Insectary room showing arrangement of plexiglass nest-boxes (covered with black oilcloth) and masses of fresh flowers necessary to maintain *Agapostemon*. Top of nests are against wall (upper nest) and horizontal shelf (lower nest) in order to take advantage of the tendency of *Agapostemon* females to search for nests along vertical and horizontal surfaces.



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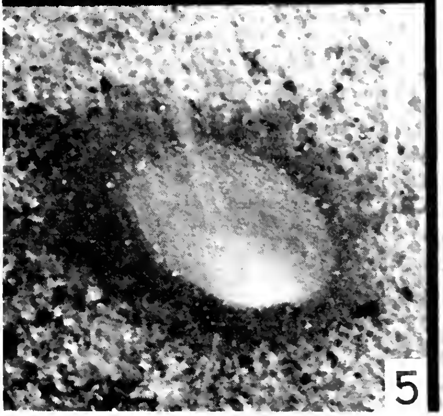

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FIG. 2. Plexiglass observation nest-box with cells and hibernacula of *Agapostemon texanus*. FIG. 3. Plate glass observation nest-box (1 meter square) with black oilcloth. FIG. 4. *A. texanus* female "guarding" burrow in observation nest-box. FIG. 5. Cell of *A. splendens* with liquid lining soaking into surrounding sand. FIG. 6. Cells of *A. texanus* in loam showing youngest cell (middle) with pollen ball, older cell with mature larva (top) and oldest cell with defecating larva (bottom).

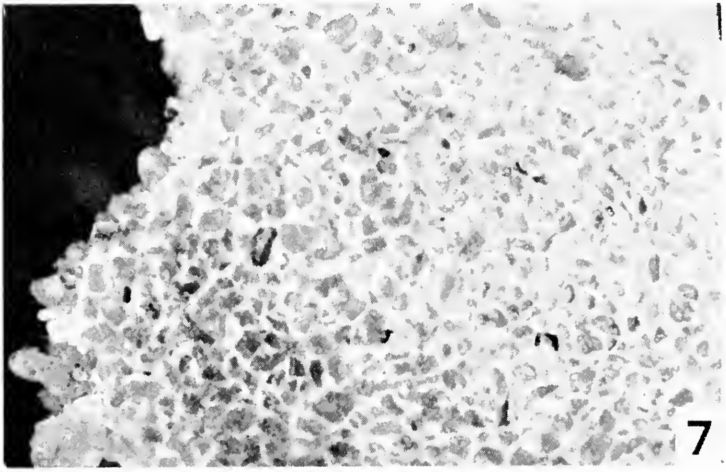
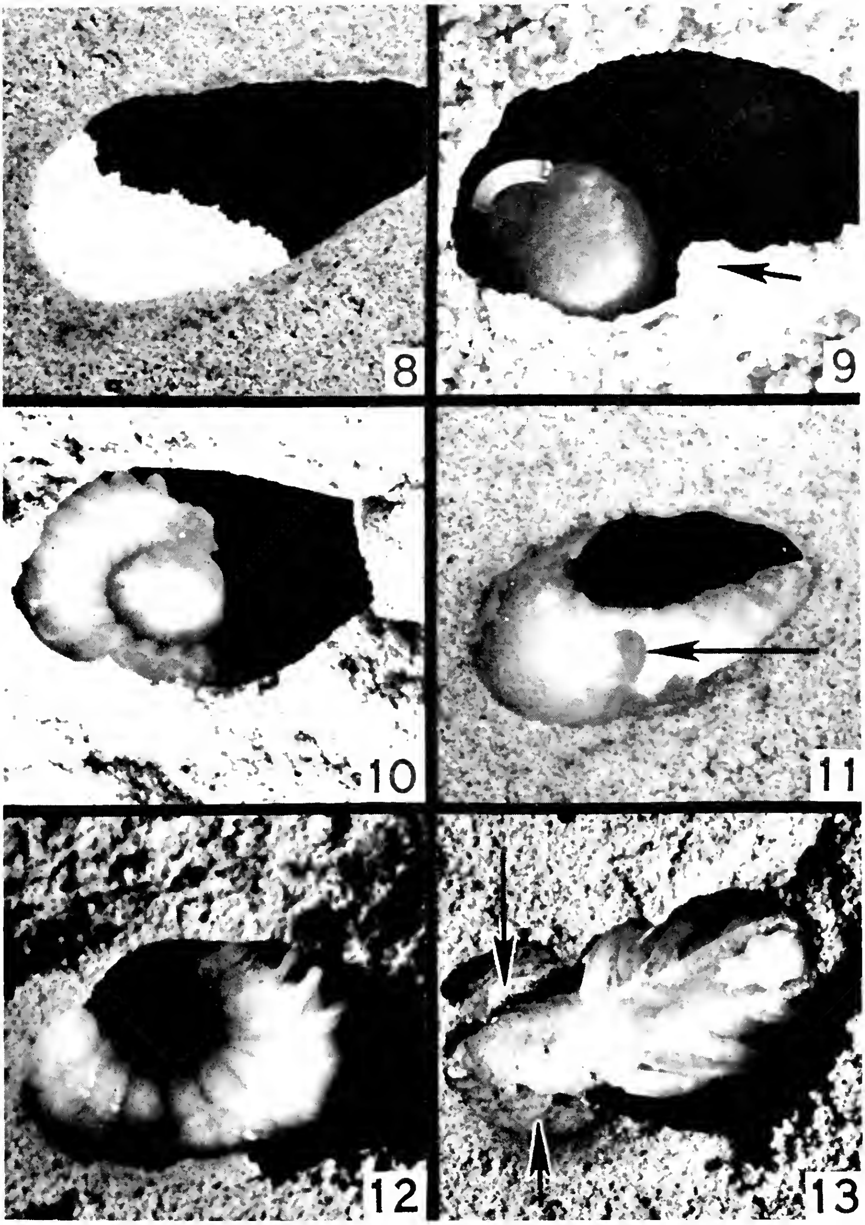


FIG. 7. View of inner wall of cell fragment of *Agapostemon splendens* showing how liquid cell lining (white) is used to coat and cement sand grains (cell is not lined with sand or loam taken from burrow walls).



FIGS. 8-13. Cells of *Agapostemon* in observation nest-boxes (background in cells blackened to increase contrast). FIG. 8. Loose pollen in partially provisioned cell of *Agapostemon texanus*. FIG. 9. Pollen ball with egg in cell of *Agapostemon splendens* with arrow indicating piece of cellophane-like cell lining detached from glass of observation nest-box. FIG. 10. Feeding larva of *A. texanus* balancing pollen ball on abdomen. FIG. 11. Defecating larva of *A. texanus* with arrow indicating feces smeared on cell wall. FIG. 12. Prepupa of *A. texanus* with characteristic mesosomal tubercles. FIG. 13. Pupa of *A. texanus* with arrows indicating moldy feces.

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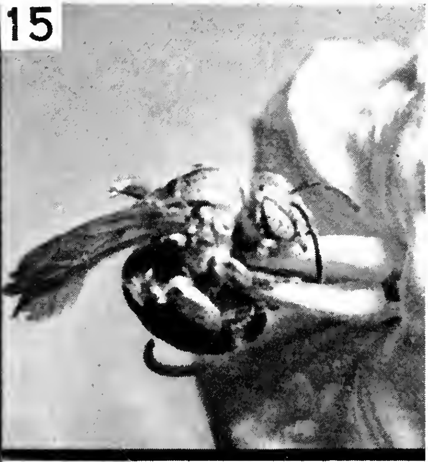

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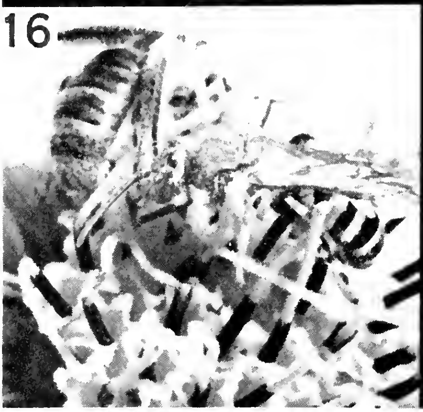

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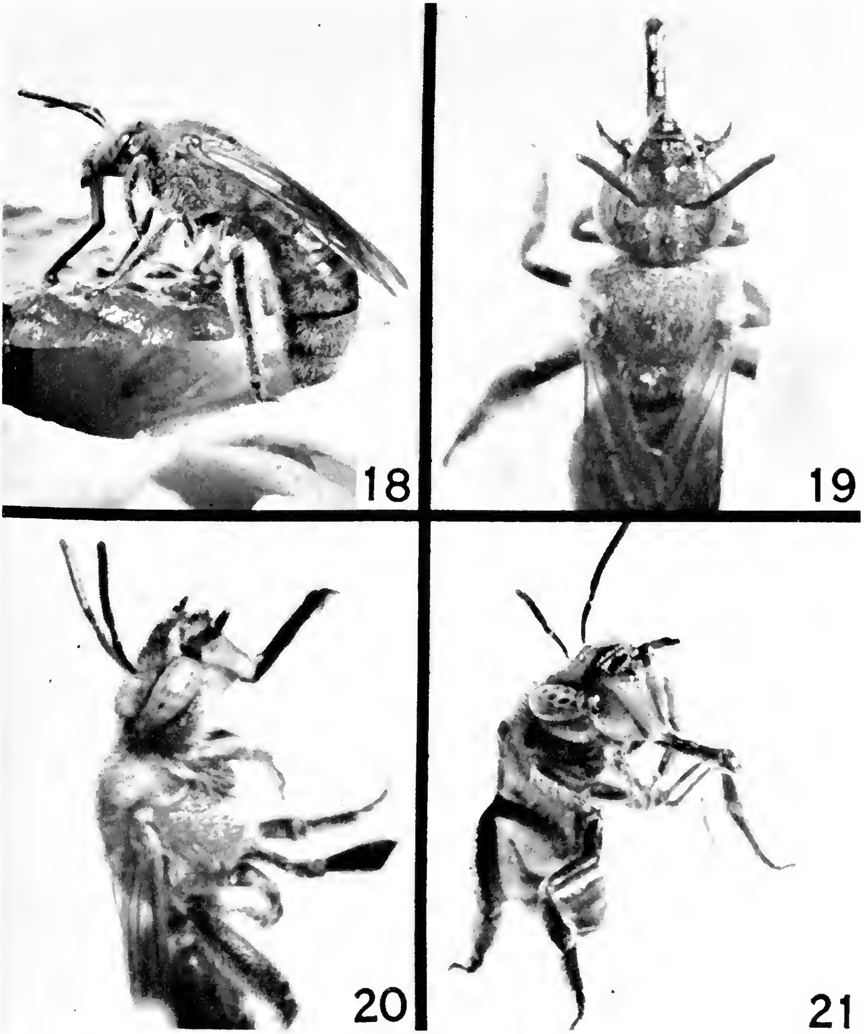
Fig. 14. Two diapausing female *Agapostemon splendens* sharing hibernaculum in observation nest-box. Note abnormal anastomosis of two burrows. Fig. 15. Female *A. splendens* "buzzing" to obtain pollen from tubular anthers of *Solanum rostratum*. Wings remain folded, mandibles and legs grasp anthers, and body is flexed while vibrating mesosoma causes pollen to spray from apical pores of anthers and adhere to underside of mesosoma. Fig. 16. Male and female of *A. texanus* foraging together on *Silphium* flower. Fig. 17. Two female *A. texanus* foraging together on *Silphium* flower.



Figs. 18-21. *Agapostemon texanus* females. Fig. 18. Imbibing honey-water on plastic flower. Figs. 19-21. Extending mouthparts (extend and retract once a second) to evaporate water from drop of nectar suspended by surface tension between genal region, basal half of proboscis, and underside of labrum. All four bees are in characteristic position with forelegs drawn together under thorax.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

VOL. XLVIII PAGES 721-765 NOVEMBER 14, 1969 No. 17

The Skeleto-Muscular System of Mecoptera: The Head[1,2]

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ABSTRACT

This is a morphological study of the skeleto-muscular system of the head of adult Mecoptera and is based on 18 genera representing 9 families. The subgena has become ventrally displaced along the lateral margin of the clypeus, with the formation of a clypeogenal suture. Most of the cranial sutures are suppressed, resulting in poorly defined cranial regions. The occipital and postoccipital regions have moved dorsally and cephalad. The maxillae are typical of chewing insects. The maxillary musculature is also of the general type but is modified in two families through a secondary shifting of the tentoriocardinal and tentoriostipital muscles. The tergolacinial muscles are bifurcate in origin but insert on a common apodeme. The stipitopalpal muscles are unique to Mecoptera among the orders of the Panorpoid Complex. There is an overall reduction in the number of maxillary muscles. The mandibles are variable in shape but constant in articulation. The articulations include an intimate connection between the hypocondyle and subgenal wall and between the epicondyle and the Apodemalwalze, which is unique to Mecoptera. The number of mandibular muscles is reduced. There is no gula in Mecoptera but there is a well developed postgenal bridge which results in a reduced labial base. The retention of a membranous postmentum and a sclerotized mental plate is regarded as secondarily derived. There are no ligular elements in Mecoptera. The labial musculature is extremely variable but the trend is toward reduction. The hypopharynx is closely associated with the labium and the pharyngeal trough and is not musculated. The antennae are of the flagellar type and are only unusual in the possession of a rotator muscle of the scape in some families and an extensive antacorium. The tentorium is composed of five elements, of which only the corporotentorium is variable, and in some families it completely divides the occipital foramen into

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[2] A portion of this work was supported by NSF Grant GB-7045X to Dr. George W. Byers, Dept. of Entomology, The University of Kansas.

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two foramina. There is no mesal fusion of the tentorial arms. Compared to generalized insects, the modifications of the mecopteran head involve a reduction of the gnathal elements into a new kind of sucking organ; otherwise, many primitive features are retained. All of the structures present can be homologized with similar structures in other orders of insects.

INTRODUCTION

Very little has been done on the anatomy of Mecoptera probably because there was not available material of all families of Mecoptera. What was available was examined in detail, particularly by German morphologists during the 1930's. Heddergott, Bierbrodt, Hasken, and Grell studied Panorpidae extensively. The Japanese workers, Miyake and Issiki, contributed large works on Panorpidae of their region. As a consequence of these studies, a great body of anatomical information was developed on Panorpidae. Unfortunately, as will be repeatedly shown in this paper, the Panorpidae are exceptionally specialized and do not represent the order Mecoptera as a whole.

At its inception, the principal aim of this study was to gather evidence with which to reconsider the position of Mecoptera within the Panorpoid Complex. In the course of the study it became apparent that there were basic problems in the anatomy of Mecoptera that had to be solved before the Mecoptera as an order could be compared with the other orders in the Panorpoid Complex. The point of emphasis shifted to a comparative investigation of the order as a whole, with the hope that there was a basic pattern within the skeleto-muscular system of the order. Presumably, such a pattern could then be compared with those of other orders at a later date. It also seemed desirable to have a basic knowledge of the order as a cohesive unit, regardless of the Panorpoid Complex arguments.

Before undertaking a comparative study, it was necessary to determine whether there is in fact a "genus blueprint" and a "family blueprint"—that is, whether all of the members of a given genus are anatomically equivalent in terms of their skeleto-muscular system and then whether all of the genera of a given family are equivalent in the same way. This task began with the Bittacidae, which contains the largest number of genera. The findings of this study demonstrated that a given species would adequately serve as a representative of the family as a whole and not simply as a representative of itself. The remaining families are small, being usually monogeneric or digeneric. The assumption that any one species would serve as a family representative was carried over from the bittacid study. Family recognition was based on a recently proposed classification by Byers (1965) which splits the order into the largest number of families (nine) to date. At the present this classification is acceptable and is based on a variety of evidence including morphological, ethological as well as ecological (most of which is still unpublished). Species on which this study is based are as follows:

- Panorpidae
  - *Panorpa nuptialis*
  - *Panorpa communis* (from the literature)
  - *Neopanorpa harmandi*
- Bittacidae
  - *Bittacus chlorostigma*
  - *Bittacus pilicornis* (from the literature)
  - *Apterobittacus apterus*
  - *Harpobittacus australis*
  - *Harpobittacus tillyardi*
  - *Pazius obtusus*
  - *Anabittacus iridipennis*
  - *Kalobittacus microcerus*
  - *Austrobittacus anomalus*
  - *Neobittacus blancheti*
- Apteropanorpidae
  - *Apteropanorpa tasmanica*
- Choristidae
  - *Chorista australis*
- Meropeidae
  - *Merope tuber*
- Boreidae
  - *Boreus unicolor*
  - *Boreus californicus*
- Nannochoristidae
  - *Nannochorista dipteroides*
- Notiothaumidae
  - *Notiothauma reedi*
- Panorpodidae
  - *Panorpodes paradoxa* (from the literature)
  - *Brachypanorpa carolinensis*

The investigation treats the order Mecoptera as a whole in terms of its skeleto-muscular system. In the course of interpreting structure, certain problems arose, most of which stem from older problems in general insect morphology and are not specific to Mecoptera. For example, the details of the preoral cavity of insects have never been adequately treated morphologically, and so it is not surprising that taxonomists have retained morphologically unsatisfactory terminology in this regard. In other cases it seemed that a functional point should take precedence over the homological, at least for the present, and in those instances references are included to sources which consider arguments in the classical manner.

An obvious characteristic of the head of Mecoptera is the modified feeding apparatus or proboscis, which is customarily termed the rostrum. Unfortunately, not enough is known about the feeding habits of the order to discuss feeding in any detail, but the rostrum is considered in a different way. One objective has been to consider the rostrum as a modification of a generalized insect head, and I looked for the changes that would have been necessary to convert a generalized head into a mecopteran head in the most efficacious manner. There is no intention of proposing a phylogeny here but merely an argument as to how a generalized head (real or imagined) could be so rearranged.

The problem of terminology usually involves a choice between traditional names (even though perhaps morphologically incorrect) and names based on function, which are often just as subjective. Two courses have been followed here: the names of the skeletal elements are based on the designations of Snodgrass (1935, etc.) while those of musculature are based primarily on the designations of Matsuda (1965), the most recent comprehensive and comparative treatment of head musculature in insects.

The list of structures illustrated may appear to favor one taxonomic group or another. They were chosen most often with an eye to making a point; other times, certain groups were illustrated simply because they were not previously illustrated and they demonstrate variations in certain features.

ACKNOWLEDGMENTS

This study could not have been done at all, save for the kindness and interest shown me by Dr. George W. Byers of The University of Kansas. Along with Dr. C. D. Michener and Dr. R. W. Lichtwardt, also of The University of Kansas, he critically reviewed the manuscript. In addition, he materially supported this study by way of NSF Grant GB-7045X. I also express thanks to Dr. C. W. O'Brien and Dr. L. B. O'Brien who collected a great deal of material for me.

METHODS AND MATERIALS

Most specimens used had been preserved in a variety of the common fixatives such as 70% ethanol, Bouin's solution, Kahle's solution, or Dietrich's solution, depending on the source of the material. In some instances pinned museum specimens were used for examination of external features.

Fluid-preserved specimens were dissected in 70% ethanol, with razor blade fragments and jewelers' forceps, under a standard dissecting microscope. Occasionally the tissues required histological staining to accentuate certain features of skeleton and musculature. After initial dissection, specimens were placed in a 0.5% solution of Congo red and 70% ethanol for 30 minutes, washed in 70% ethanol and then examined. The residual effect is that the stain partially washes out of the muscles but is retained by the endoskeleton. This greatly facilitated locating origins and insertions of muscles. A solution of 0.5% methylene blue in 70% ethanol was also used for high-lighting muscles, but this stain has no residual effect.

The highest magnification of the dissecting microscope (90 x) was occasionally insufficient for the positive identification of certain muscles; for example, the rotator of the scape is quite small (length about 300 μ) and is surrounded by deposits of fatty tissue. Examination of muscles of this magnitude required that sample tissues be temporarily slide-mounted for examination under a compound microscope, so that the muscle fibers could be clearly identified.

The examination of the musculature of most of the gnathal appendages required careful dissection under a dissecting microscope, followed by temporary mounts and examination under a compound microscope. In these cases the specimens were stained previously with Congo red for ease in muscle identification.

The external skeletal morphology was examined in several ways. In some instances pinned specimens were sufficient (and in some cases were the only ones available) to yield gross information. Fine details of external structure and the details of internal skeletal structure were usually elucidated by boiling the specimen in a 10% KOH solution and washing in 70% ethanol. After such treatment the specimens are often too hyaline to discern fine elements, and the specimen must then be stained. Again, Congo red proved useful. If a specimen is first stained in Congo red, washed, and then boiled in a 10% KOH solution, the soft tissues are rendered while the cuticle retains the stain perfectly. In those specimens which were not boiled but simply stained for muscle work, the residual stain was particularly concentrated along apodemes and apophyses, presumably owing to chemical differences in these areas. No attempt was made to identify the cuticular layers, but this reaction is useful in following apodemes.

Where possible, drawings were made after the examination of several individuals to avoid being misled by teratological specimens. The illustrations were made by use of an ocular grid and grid paper. The techniques used in such a study are not easily described in formula fashion since each group has its own tricks which the student of morphology must stumble through before mastering; for example, the amount of pressure that one can apply to a muscle band before it separates from its origin or insertion, or the care needed in dissecting specimens that have been preserved for 20 or 30 years.

Perhaps the greatest difficulty was obtaining material. This has undoubtedly been the reason why earlier morphologists did not treat Mecoptera in more detail. The difficulty in getting representatives of each family occasionally led to only a single specimen being used; for example, all of the information presented here on Notiothaumidae is based on a single preserved specimen.

Perhaps it should be noted that, in the ensuing account, each feature of Mecoptera is compared with insects in general. While this has led to the inclusion of information available in sources such as Snodgrass (1935, etc.), it seemed justifiable to include this information so that a clearer picture of Mecoptera could emerge and that the Mecoptera as a whole could be seen in the context of general insect morphology.

LIST OF ABBREVIATIONS

abt	abductor tendon of mandible
act	antacorium
adt	adductor tendon of mandible
af	alaforamen
aj	antennarium
an	antenna
anf	antennifer
ans	antennal suture
apm	anterior dilator of the pharynx
aw	Apodemalwalze
c	clypeus
ccm	clypeocardinal muscle
cdm	clypeoapodemal adductor
cgs	clypeogenal suture
co	compound eye
cos	circumocular suture
cr	cardo
csm	clypeostipital muscle
ct	corporotentorium
dfm	distal flexor of the palp
dpm	depressor of the pedicel
dsm	depressor of the scape
eci	epicondyle
ecl	ecdysial cleavage line
eph	epipharynx
epm	extensor of the labial palp
es	epistomal suture
f	frons
fl	flagellum
fo	foramen magnum
fpm	flexor of the palp
g	gena
gl	galea
hc	hypocondyle
hy	hypostoma
hyb	hypostomal bridge
hyp	hypopharynx
i	lacinial bridge
j	lateral process of anterior arm
k	stipital process
l	labium
lc	lacinia
lct	lacinial tendon
lem	labroepipharyngeal compressors
li	lateral ocellus
lp	labial palp
lpg	labial palpiger
lpm	levator of the pedicel
lsm	levator of the scape
lr	labrum
mbm	tergal abductor of mandible
mdm	tergal adductor of mandible
mlc	maxillo-labial complex (zygostipes)
mn	mandible
mp	mental plate
mx	maxilla
mxf	maxillary palpifer
mxp	maxillary palp
nf	neuraforamen
oc	ocular sclerite
occ	occipital condyle
oi	median ocellus
pe	pedicel
pg	postgena
pgb	genaponta
pha	pharyngeal aperture
pht	pharyngeal trough
pk	postmentum
pl	pleurostoma
po	postocciput
pos	postoccipital suture
ppm	posterior dilator of the pharynx

q	anterior tentorial arm
qt	anterior tentorial pits
r	rostrum
ra	retractor apodeme
rk	prementum
rnm	premental retractor muscle
rsm	rotator of the scape
sc	scape
sg	subgena
sgs	subgenal suture
spm	stipitopalpal muscle
ss	subantennal suture
st	stipes
tcm	tentoriocardinal muscle
tlm	tergolacinial muscle
tna	tentorium
ts	temporal suture
tsm	tentoriostipital muscle
ua	galeal apodeme
v	dorsal tentorial arm
vx	vertex
w	posterior tentorial arm
y	lacinial apodeme

CRANIAL SUTURES— INTRODUCTION

There has been a great deal of controversy in the literature over the true meaning of the term "suture" and the criteria for recognizing one. The difficulties attending this problem stem mainly from differences of interpretation of various stages during ontogenetic development. Most recently, Snodgrass (1960) distinguished three basically different kinds of sutures as distinct from suture-like lines termed sulci. As a purist, he restricted the term suture in insect morphology to lines of fusion between sclerites, preferably intersegmental ones. On what appear to be only etymological grounds, he used the term sulci for all lines of inflection other than intersegmental ones.

Matsuda (1965) summarized the history of these terms as well as the contributions of Hinton, DuPorte, and others in resolving these difficulties. He presented arguments based on comparative anatomy and embryology advanced by various authors to support various interpretations of these lines of inflection. Matsuda most notably pointed out that there can be several different origins of sutures in an unrestricted sense.

There are still differing homological and functional interpretations of various sutures. If a primarily topographical viewpoint is taken, then homological significance of these sutures is largely irrelevant, and the same may be said for the functional interpretation. I have taken a combined functional and topographical viewpoint and will make no terminological distinction between sutures and sulci in the sense of Snodgrass. They are often functionally the same regardless of the ontogenetic and historical sequences by which they arose.

ECDYSIAL CLEAVAGE LINE

The ecdysial cleavage line (epicranial, frontal, or coronal suture of various authors) was shown by DuPorte (1946) not to be a suture of any kind but only a line of weakness in the larval cranium to facilitate ecdysis, and having essentially no morphological significance in the adult cranium.

DuPorte's interpretations have been subsequently corroborated by Snodgrass (1947, 1960) and Matsuda (1965). This line lacks the essential element of any suture, an internally defined ridge or apodeme. There is a tendency for this line to become suppressed in the adult cranium of pterygote insects (Snodgrass, 1935, 1947, 1960).

This trend is borne out in adult Mecoptera where the ecdysial cleavage line is either entirely suppressed or greatly reduced and confined to the ocellar region (Figs. 21-29). The line is present in the adult cranium of Panorpidae, Panorpodidae, and Choristidae. Issiki (1933) incorrectly recorded it as absent from the Panorpidae. Heddergott (1938) correctly observed its presence in Panorpidae and noted that it lacks an internal apodeme. In the Panorpodidae (Fig. 25), the ecdysial cleavage line (ecl) is more extensive than in Panorpidae but it is still greatly reduced from the larval condition. In the Choristidae (Fig. 29), the line is faint and occurs as a light furrow in the ocellar region. There is no trace of an ecdysial cleavage line in the adult cranium of any other families of Mecoptera although it is present in the larvae and pupae of those families which have been checked (Applegarth, 1939, the Bittacidae; Steiner, 1930, Yie, 1951, Bierbrodt, 1942, the Panorpidae and Panorpodidae). Setty (1940) noted the absence of the ecdysial cleavage line in adult Bittacidae.

In the only comparative study of the head of adult Mecoptera, Otanes (1922) alleged that the ecdysial cleavage line (which he termed the epicranial suture) is "undoubtedly the most important landmark on the head capsule of insects." This error may be excused since it predated DuPorte's (1946) developmental study of ecdysis and his elucidation of the significance of this line. Otanes noted the state of this line in the adult cranium of Meropeidae, Panorpidae, Panorpodidae, Bittacidae, and Boreidae but did not advance any argument to support his claim for the importance of the ecdysial cleavage line.

EPISTOMAL SUTURE

The epistomal or frontoclypeal suture is possibly a primary formation during ontogeny that indicates the posterior border of the acronal clypeolabrum (Matsuda, 1965). If this interpretation is correct, it would qualify this line of inflection as a suture in the sense of Snodgrass (1960). The developmental basis for this interpretation has been discussed by Matsuda. The epistomal suture (es) traverses the lower region of the face between the anterior tentorial pits (qt) and joins the upper ends of the subgenal sutures (Figs. 21-29, sgs). Internally, it forms a distinct ridge or apodeme and is the boundary between the clypeus (c) and the frons (f). The functional significance of this suture in Mecoptera lies in its close association with the anterior tentorial pits, where it reinforces the cranial capsule. Whether this is primitively so has been disputed by DuPorte (1946).

Morphologists have generally used three criteria for distinguishing the frons and clypeus, none of which is constant for the insects (Matsuda, 1965). The disparity between ontogenetic interpretations and arguments based on final products is apparent here. As mentioned earlier, an ontogenetic interpretation suggests a clypeo-labral relationship, but in the completed cranium this is not apparent. Matsuda (1965) discussed the arguments pertinent to the recognition of the frons and clypeus and accepted Snodgrass' (1947) interpretation, which is that the frontal ganglion is a convenient landmark between these two areas. While this definition is consistently operative, it is questionable since it rests on the grounds that it is extremely unlikely that the position of the frontal ganglion would have changed during the course of ontogeny or phylogeny. Since this suture is often suppressed in higher insects, a distinction between frons and clypeus is often only theoretical (Matsuda, 1965).

In his studies on Mecoptera, Miyake (1913) distinguished the frons and clypeus correctly. Otanes (1922) reverted to the position of a single fusion product, the frontoclypeus, on the grounds that the epistomal suture is absent in the forms he studied, which is not true. That the epistomal suture is present in all Mecoptera (at least in apodemal form) and that it is a reliable indication of the limits of a distinct frons and clypeus was demonstrated by Hetrick (1935). He showed that the epistomal suture is always at the level of the frontal ganglion in Mecoptera and that the pharyngeal dilators and buccal muscles are respectively above and below this line, which is characteristic of insects in general (Snodgrass, 1935, 1947). The anterior tentorial arms pass between the ventral buccal muscles (which generally arise on the clypeus) and the dorsal pharyngeal dilators (which generally arise on the frons), with the frontal ganglion and the epistomal suture disposed between them.

The epistomal suture of Mecoptera is variously developed. It is present both as a suture and an apodeme in Panorpidae, Apteropanorpidae, Nannochoristidae, Notiothaumidae, and Choristidae. The suture is barely retained in Bittacidae and Panorpodidae, but its apodeme is clearly defined. In Boreidae and Meropeidae the epistomal suture is present only as an apodeme, with no indication of an external suture. When externally visible, the suture varies from almost straight to strongly curved (Figs. 21-29). The extreme arching is correlated with the mesal migration of the tentorial arms, without shortening of the suture. In fact, the suture is longer in those forms in which the tentorial arms have moved closer together than in those in which it is straight.

Heddergott (1938) recognized the correct relationship between frons and clypeus in Panorpidae; Setty (1940) in Bittacidae; and Evans (1942) in Nannochoristidae. I have corroborated their findings as well as established this relationship in the other families.

SUBGENAL SUTURE

The subgenal suture is a lateral continuation of the epistomal suture on both sides of the cranium. It is considered to be of secondary origin, in the Snodgrass sense, in response to structural need (Matsuda, 1965). Its internal ridge reinforces the area above the mandibles and sets off a subgenal area below it. The sclerotized portion of the head capsule directly above the base of the mandible is termed the pleurostoma, that behind, the hypostoma. These designations are entirely arbitrary since there is no suture between them. There is a tendency for this suture to be suppressed in the higher Pterygota (Matsuda, 1965). The status of the subgenal suture in Mecoptera is complicated by the ventral elongation of the head, since the normal relationship between the gena and clypeus has changed by the elongation of the subgena along the lateral margin of the clypeus (a situation which appears to be unique to Mecoptera).

The subgenal suture is present both externally as a line and internally as an apodeme in all Mecoptera except Apteropanorpidae and Notiothaumidae (Figs. 21-26, 29, sgs). When present, this suture is not easily defined externally (but is visible), but its internal apodeme is distinct. The situation is obscure in only one family, the Panorpodidae, because the rostrum is shortened and so rugose that it is not possible to distinguish the wrinkles from the sutures in this area.

CLYPEOGENAL SUTURE

There is a new suture, formed along the fusion of the clypeus and subgena, which appears to be identical to a similar suture described by DuPorte and Bigelow (1953) and Bigelow (1954) in Hymenoptera. This is termed the clypeogenal suture. According to these authors the genal area (of Hymenoptera) has descended along the lateral margin of the clypeus and the new clypeogenal suture represents the fusion line. The same suture occurs in some of the lower Pterygota.

This suture is distinct and should not be confused with the subgenal suture. Miyake (1913) and Issiki (1933) both realized the distinctness of these two sutures, discussed and illustrated both, but did not name the clypeogenal suture. They did correctly observe that the clypeogenal suture extends latero-ventrad of the anterior tentorial pits and that it terminates in the area between the two mandibular articulations on either side of the head. The clypeogenal suture is present in all Mecoptera (Figs. 21-29, cgs). Some of the more recent workers (Heddergott, 1938; Ferris and Rees, 1939; Evans, 1942; Setty, 1940) either ignored or misunderstood this suture. Heddergott, for example, confused the clypeogenal and subgenal suture in Panorpidae. Setty (1940) ignored both, although they are present in Bittacidae. Evans (1942) described the subgenal suture in Nannochoristidae but missed the clypeogenal suture.

FRONTOGENAL SUTURE

Another suture that commonly occurs in insects is the frontogenal suture, which extends from the anterior mandibular articulation to the ventrolateral angle of the antennae. The suture is unusual in that there has been a tendency for a high degree of development in the higher Pterygota (Matsuda, 1965). Its morphological significance lies in that it might have been the primitive site of the anterior tentorial arms (DuPorte, 1946), although this interpretation has not been universally accepted (Snodgrass, 1960). Although this suture does not occur in any mecopteran adults, it is present in other orders of the Panorpoid Complex (Crichton, 1957, in Trichoptera); its absence is a major deviation from the pterygote tendency to preserve and develop the extent of this suture. I cannot correlate the absence of this suture with any particular modification of the mecopteran head.

CLYPEOLABRAL SUTURE

In many insects there is a clypeolabral suture separating the clypeus and labrum. This suture is present in the larvae and pupae of Mecoptera (Bierbrodt, 1942) but is absent from the adults, as correctly reported by Otanes (1922), Hetrick (1935), Issiki (1933), Heddergott (1938), and Setty (1940). I have found it absent also from those families which the cited authors did not investigate. There are few criteria for the recognition of the labrum as distinct from the clypeus. These are the presence of the clypeolabral suture and the labral depressors. Although Mecoptera lack a clypeolabral suture, the labral depressors are present.

POSTOCCIPITAL SUTURE

The postoccipital suture is generally regarded as an intersegmental suture between the maxillary and labial segments (Matsuda, 1965) and satisfies Snodgrass' criteria for a true suture. This suture is functionally important because it gives rise to the posterior tentorial arms and also serves as a site for muscle attachment. It is present in all Mecoptera (Figs. 30-38, pos). Posteriorly it delimits the postocciput and is discussed with that feature and the tentorium. Intimately associated with the postoccipial suture is the occipital suture which primitively separates the maxillary and mandibular segments. Matsuda (1965) noted that this suture becomes suppressed in the higher Pterygota and there is no indication of an occipital suture in Mecoptera. Evans (1942) misinterpreted an unusually well developed postocciput as the occiput, in Nannochoristidae, and confused the postoccipital suture as an occipital suture. That this suture is not the occipital suture in Nannochoristidae is indicated by the fact that the posterior tentorial arms arise from it.

CIRCUMOCULAR SUTURE

The periphery of the compound eyes is indicated by the presence of a circumocular suture which sets off an ocular sclerite surrounding the eye (Figs. 28, 41). This suture is present in all Mecoptera and is highly developed both externally as a line and internally by the ridge it forms. The only unusual modification of this area is that in Boreidae the ocular sclerite is anteromedially incised.

TEMPORAL SUTURE

At the dorsolateral angles of the postoccipital suture there is a short suture (labeled "loc" by Issiki) which extends anteriorly on either side approximately parallel to the edge of the compound eye (Figs. 39, 41-43). This unusual suture occurs in Mecoptera (except Nannochoristidae and Bittacidae) and was first described in the Panorpidae by Issiki (1933). Issiki homologized it with similar sutures on the posterior part of the cranium that terminate on the occipital suture (absent from all Mecoptera) and laterally separate the occiput from the postgena in two primitive groups, the Micropterygidae (Lepidoptera) and the Rhyacophilidae (Trichoptera). Issiki argued that the area partially enclosed by these sutures represented the occiput of other insects, which would normally occur in the same place on the back of the cranium. This implies that the occiput of Mecoptera has migrated from a primitively posterior position to a dorsal position. I am in complete agreement with this interpretation.

Although there is no occipital suture in Mecoptera, the postoccipital suture has retained its normal position. In addition, in the process of rostrum formation (as will be discussed later), there has been a complete antero-ventral reorganization of the mecopteran cranium, and it is reasonable to expect the occiput (though not clearly defined) to have participated in this rearrangement. Homologous sutures have been reported in Lepidoptera by Ehrlich (1958) and in Mantodea by Levreault (1936).

SUBANTENNAL SUTURE

In Boreidae, Panorpidae, Panorpodidae, and Meropeidae there is a fine subantennal suture present internally as a ridge extending from the lateroventral side of the base of the antenna to the subgenal suture (Figs. 24, 26). The apodeme formed by this suture would appear to contribute to the strengthening of the head capsule against vertical stresses on the area between the antennal bases and the compound eyes, as the antennae are rather large in Mecoptera and the antennal muscles fairly well developd. This apodeme should also contribute a modicum of support for the cranium against the lateral pressures exerted by the contraction of the mandibular muscles.

CRANIAL REGIONS—Introduction

It is necessary to have a consistent account of the sutures in a cranium before cranial sclerites or regions can be defined. In defining areas of the cranium, one should realize what criteria can be used for their recognition and, secondly, what significance (real or imagined) can be attached to these areas. A functional interpretation will not necessitate rigid accounting for missing parts. In a more classical approach, the various cranial areas are always defined by sutures (Snodgrass, 1935), and when these sutures are suppressed, as is often the case, the limits of otherwise well defined cranial areas become obscured and for the most part entirely arbitrary. Unfortunately, too much argument has been devoted to the recognition of arbitrary cranial regions in the heads of insects (such as Mecoptera) in which these sutures have been suppressed. The important functional aspects of these sutures are their internal apodemes, which provide muscle attachment and structural reinforcement.

There are a variety of ways in which the insect cranium can be subdivided. Since most are arbitrary, I have selected one that is more functionally oriented than the others, that of Snodgrass (1935). According to his system, the functional areas of the insect cranium are the frontoclypeal area, the lateral parietal regions, the occipital arch, the postoccipital area, and the subgenal areas basad of the gnathal appendages. Of these regions, only the occipital arch is absent from Mecoptera.

Frontoclypeal Region

The frontoclypeal region in insects is situated between the frontal sutures (when present) or the compound eyes or antennae and ventrally bounded by the base of the labrum (when distinct). If an epistomal suture is present, the area is further reduced to a dorsal frons and a ventral clypeus (Snodgrass, 1935). There are no frontal sutures in Mecoptera and the antennae have moved ventrally. In some instances only the apodeme of the epistomal suture is present in Mecoptera (Figs. 21-29). The frons usually bears the median ocellus and is the point of origin for the labral muscles (Snodgrass, 1935). In Mecoptera the same relationship exists except for the two families which lack ocelli (Meropeidae and Apteropanorpidae). Because the antennae are anteromedially displaced, Issiki (1933) designated the area above the antennae as the postfrons and that below, the antefrons. There is no justification for the retention of these terms since there is no suture to demark the divisions. For the same reasons it is difficult to retain Issiki's subdivision of the clypeus into an anteclypeus and a postclypeus (terms borrowed from Crampton, 1921), since there is no suture separating the two. In Mecoptera there is no distinct limit of the frons except the epistomal suture.

The clypeus of Mecoptera is an elongate sclerite which contributes to the formation of the anterior side of the rostrum. As might be expected, its relative length varies with the length of the rostrum. The clypeus of all Mecoptera is constricted at the level of the hypocondylar mandibular articulation. That portion above the mandibles is subquadrate; that below the mandibles is gradually tapered to a point in those families having long and intermediate rostra, while in those families having a short rostrum the clypeus is approximately quadrate (Figs. 21-29).

There is no clypeolabral suture in Mecoptera but there is an apodeme which separates these parts, as was initially shown by Miyake (1913), but with some errors. Miyake thought that the clypeal constriction at the mandibular bases represented the junction of labrum and clypeus in Panorpidae, but his interpretation of other families was correct. Issiki (1933) questioned this interpretation and Heddergott (1938) correctly described the situation in Panorpidae. Heddergott made the same mistake as did Issiki in his interpretation of an anteclypeus and a postclypeus and in thinking that the clypeal constriction separated the two. Both Issiki and Heddergott did, however, point out that the labrum has become laterally displaced by the ventral extension of the clypeus. The apex of the clypeus is heart-shaped and supports the membranous labrum. The labrum then lies laterad of the clypeus and ventrad of the mandibular bases. The clypeolabral apodeme varies from a well developed ridge to a barely perceptible line. A proximal or basal limit of the labrum is indicated by the insertion of the labral compressor muscles (discussed later).

PARIETAL REGION

The parietals are lateral parts of the cranium delimited dorsally by the coronal suture, anteriorly by the frontal suture, and posteriorly by the occipital suture when these sutures are present. Each of the parietals usually bears a lateral ocellus, an antenna, and one of the compound eyes. In generalized insects the dorsal parts of the parietals form the vertex and the portions posterolateral to the eyes form the genae (Snodgrass, 1935).

The limits of the parietals as described for generalized insects are not present in Mecoptera. The only indication of a dorsal limit of the parietals occurs in those Mecoptera which retain temporal sutures. A definitive vertex and genae do not exist in Mecoptera. There is no occipital suture in Mecoptera. The coronal portion of the ecdysial cleavage line is a reduced trace confined to the ocellar region in Choristidae, Panorpidae, and Panorpodidae.

These areas are arbitrary because they are not defined by sutures, a condition also found in Hymenoptera and Diptera (Heddergott, 1938). The vertex might arbitrarily be defined in the absence of sutural limits as that area mesal and dorsal to the lateral ocelli. The genae can be considered as approximately ventrolateral to the compound eyes and unseparated from the vertex (Figs. 39-47). Heddergott (1938) realized the true relationship between the gena and subgena and that the lateral margins of the rostrum are formed by the subgenae; however, he misinterpreted the clypeogenal suture as a continuation of the subgenal suture. He also pointed out that the postgenae are fused with the occiput and the vertex through the suppression of both the occipital and postgenal sutures.

Posterior Region

In Mecoptera, the head approximates the orcephalic type in which the orientation is hypognathous and the foramen magnum (or occipital foramen) is subdivided by the corporotentorium into a dorsal alaforamen and a ventral neuraforamen. The foramen is dorsolaterally confined by the postoccipital suture and ventrally by the fusion of the postgenal processes. The postocciput bears a laterally projecting occipital condyle (or odontoidea) above the level of the corporotentorium which extends a short distance into the foramen. These condyles articulate with the cervical sclerites. As usual, the posterior tentorial pits are situated at the ventral extremity of the postoccipital suture and are closed but visible (Figs. 30-38).

There is no corporotentorium in Apteropanorpidae, Choristidae, Meropeidae, and Notiothaumidae, but it is present in the other Mecoptera; hence the Mecoptera fall into two groups, those with double foramina and those with a single occipital foramen. I can think of no explanation based on function why this should be so. The usual explanation of modification for rostrum formation does not apply because some families with short rostra and others with long rostra have double foramina while those of intermediate length do not.

Occasionally the postoccipital suture extends below the posterior tentorial pits enclosing a sclerotized area known as the gula (Snodgrass, 1935). Each portion of the postoccipital suture ventrad of the foramen is designated as the gular suture and accompanies the prognathous condition of some Coleoptera and Neuroptera. The presence of a gula in Mecoptera has been claimed by some mecopterists (i.e., Heddergott, 1938, for the Panorpidae; Imms, 1944, for the Nannochoristidae) who thought that a gula was squeezed in between the mesally projecting postgenal processes. The nature of the insect gula was not satisfactorily known until DuPorte (1962) studied the problem in detail. He showed that the gula can be either of cervical origin or in combination with postoccipital and postgenal contributions.

It should be noted that in Panorpodidae, Choristidae, and Notiothaumidae the incomplete mesal fusion of the postgenae leaves a small area, but not a gula. Evans (1942) recognized this in Nannochoristidae and pointed out that the area misinterpreted by others (Heddergott in this instance) is in reality the hypostomal bridge. This is not, however, the case in the families just mentioned. The sclerotized area enclosed by the incompletely fused mesal processes of the postgenae appears to be formed by contributions from the ventral edge of the postoccipital ridge and by the mesal extension of the posterior tentorial arms. This interpretation is only tentative and would require developmental studies for its justification.

PREORAL CAVITY—INTRODUCTION

There is an area at the apex of the rostrum ventrad of the pharynx which serves for the uptake of food into the pharyngeal aperture, or mouth. This space has been termed the buccal cavity or mouth cavity. As Snodgrass (1960) pointed out, there never has been a satisfactory treatment of this area by morphologists, and the terminology applied to it is very inconsistent. Actually, this space is the functional preoral cavity, formed by the enclosure of the gnathal appendages around it. Snodgrass considered that its upper or inner wall is the true ventral wall of the head and that the hypopharynx arises from it. The mouth (aperture of the pharynx) is anterior to the base of the hypopharynx. The depressed hypopharynx forms the floor of a pocket which has been erroneously termed the pharynx, but is now known as the cibarium of chewing insects. It is variously modified and in liquid-feeding insects is the sucking pump (Mundpumpe of the Germans) as in some Mecoptera. Because of incorrect terminology through the years (calling the cibarium the pharynx), the term "epipharynx" has been applied to the anterior wall of the preoral cavity and the implications of this term are erroneous. Unfortunately, no alternative is at hand, so the terminology is retained and the features discussed accordingly.

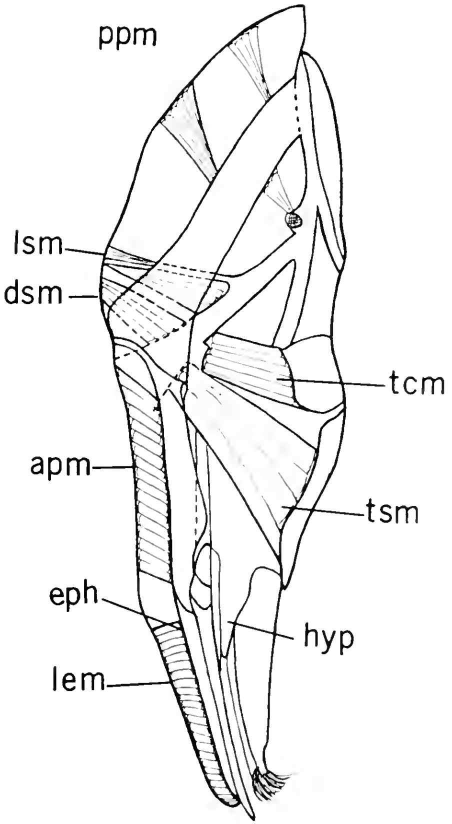
Otanes (1922) was the first to discuss these relationships in Mecoptera and used a scheme no worse than any others. He designated the pharyngeal complex as a dorsal "postpharynx" and a ventral "prepharynx"; in the latter he included the epipharynx and hypopharynx. Although this is a misuse of the term "pharynx," Otanes did adequately describe the relationships of the parts.

EPIPHARYNX

As Otanes (1922) pointed out, the size of the epipharynx varies with the size of the clypeolabrum which in turn varies with the size of the rostrum (Figs. 1-2, eph). The epipharynx of Mecoptera is a thin, membranous continuation of the posterior part of the clypeolabrum and bears a pair of epipharyngeal rods or sclerites on either side (Steiner, 1930; Heddergott, 1938). The larger pair is anterior and supports the apex of the epipharynx while the other pair is situated in the middle of the plate. At the base of the labrum there are two sclerotized rods on the posterior side which various authors have interpreted somewhat differently. Steiner (1930) suggested that these were epipharyngeal tendons, which is curious because there are no muscles attached to them. Heddergott's (1938) interpretation is that these rods represent the remnants of reduced epipharyngeal tormae, which appears more reasonable. The epipharynx has been adequately described for Meropeidae, Panorpodidae, and Boreidae by Otanes (1922) and for Panorpidae by Heddergott (1938).

The musculature of the generalized labrum as found in the lower orders (Matsuda, 1965) consists of a set of extrinsic effectors and some intrinsic compressors. Only the intrinsic labroepipharyngeal compressors (or dilators) are retained by Mecoptera (Fig. 1, lem). These muscles consist of several discrete bundles oriented somewhat obliquely and which arise on the highly sclerotized anterior labral plate and insert on the membranous, nonsclerotized opposing epipharyngeal wall. The secondary displacement of these muscles might be accounted for on functional grounds. Heddergott (1938) indicated that this arrangement facilitates sensory contact of the epipharynx with the food source to which it is appressed during feeding. The epipharynx is richly invested with a variety of sensoria which presumably function as organs of taste, an idea first advanced by Packard (1889) and further supported by Grell (1938) and Heddergott (1938). There has been no experimental work to test the nature of these receptors.

In the construction of the epipharyngeal complex, Mecoptera are referable to two distinct groups. The Panorpidae and Boreidae follow the pattern discussed above. The other Mecoptera retain only the lateral longitudinal sclerotic rods. These rods gradually become indistinct as they approach the apex of the rostrum. They are continuous with the pharyngeal trough at the level of the Apodemalwalze and the mandibular bases. The musculature of this group is identical with that of the first.



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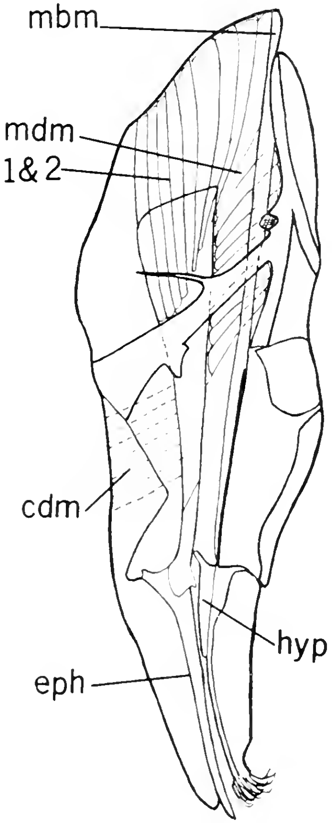

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Fig. 1. *Notiothauma reedi.* Longitudinal view showing major skeletal muscles of the head except those of the mandibles.

Fig. 2. *Notiothauma reedi.* Longitudinal view with all muscles except those of the mandibles removed.

Hypopharynx

The hypopharynx of generalized hypognathous insects forms the base of the cibarium or preoral cavity and the opening of the salivary duct is caudal to its posterior wall (Snodgrass, 1935, 1960). Matsuda (1965) indicated that embryologically the hypopharynx is a composite organ and may be formed by contributions from more than one head segment. The development of the hypopharynx in Pterygota is extremely variable and Matsuda described it as having evolved in two directions, toward reduction and toward enlargement. This organ is occasionally musculated in some of the lower orders but there is no hypopharyngeal musculature in Mecoptera. The ontogenesis of the hypopharynx in Mecoptera is not known.

Issiki (1933) adequately discussed the hypopharynx of Panorpidae and, if taken somewhat grossly, the account will serve for all Mecoptera. The hypopharynx is a simple tongue-shaped process, setose, and usually well developed in Mecoptera. It is situated between the mandibles and maxillae and hangs downward in the preoral cavity (Fig. 1, hyp). The posterior surface of its base is continuous with the lateral edges of the labium at the distal end of the mental plate. The anterior surface is laterally continuous with the flexible transverse process formed by the medial extension of the subgenae. The bridge formed by these processes is completely fused with a ventral apodemal process of the pharyngeal trough (designated the Apodemalwalze by Heddergott, etc.) and apparently unique to Mecoptera. On either side of the hypopharynx there is a thin sclerotized bar or strip that is confluent with the mesal subgenal bridge. These sclerotized processes have been subject to various interpretations. Heddergott (1938) suggested that they represent traces of the superlinguae of other insects and Matsuda (1965) used the same interpretation. Since these processes are intimately fused with the hypopharynx laterally and lack any trace of a lobed structure (as is typical of superlinguae), this interpretation should be accepted as tenuous at best, pending developmental studies.

The hypopharynx in Mecoptera is somewhat variable in length and width, but is present in all families. It is least developed in Boreidae and Nannochoristidae, in which it is reduced to a simple rounded lobe-like process. In all other Mecoptera it has the general shape already described. Representatives of several families have been illustrated by Otanes (1922), Setty (1940), and Issiki (1933). Matsuda (1965) mistakenly reported that there is no hypopharynx in Boreidae, and that the suspensorial superlinguae are present in Mecoptera.

TENTORIUM

The insect tentorium has had a long history of study, often yielding contradictory evidence. The ontogenetic contributions to the tentorium vary greatly (Snodgrass, 1960), and many theories have been proposed to account for its modifications. The history of these theories has been recently discussed by Matsuda (1965). Whatever its phylogenetic significance, the tentorium is an important structure formed by invaginations of the head capsule. Heddergott (1938) pointed out that there is a separation of the pterygote tentorium and hypopharynx in which the tentorial apophyses are volumetrically reduced and the hypopharynx is increased in volume. This does not occur in Mecoptera, where the tentorium is well developed, and the hypopharynx is ventrally displaced and greatly reduced.

The mecopteran tentorium (Figs. 30-34) is composed of the following parts: 1) a corporotentorium (ct); 2) two posterior tentorial arms (w); 3) two anterior tentorial arms (q); 4) two dorsal tentorial arms (v); 5) two lateral processes of the anterior arms (j). The corporotentorium (metatentorium of some authors) is situated in the posterior part of the head. It is variously developed in Mecoptera and may form a complete bridge across the occipital foramen, dividing it into a dorsal alaforamen (Fig. 30, af) and a ventral neuraforamen (nf), or it may remain as protruding but unfused processes extending into the undivided occipital foramen (fo). When the occipital foramen is divided, the alaforamen accommodates the alimentary canal and the neuraforamen the nerve cord and salivary ducts. The ventral margin of the occipital foramen, or of the neuraforamen, is reinforced by contributions from the genae, across the back of the head, termed the genaponta. The lateral margins of the foramen are reinforced by ridges from the posterior tentorial arms, which are buttressed caudally and dorsally at their bases, an unusual condition in insects. The fusion of the posterior arms with the postocciput is such that there is no external opening marking their termination.

The anterior tentorial arms are formed by invaginations in the epistomal area. Whether they always arise in this way has been subject to dispute (DuPorte, 1946). Whatever the case, in Mecoptera the anterior tentorial arms are always associated with the epistomal suture and are externally indicated by the anterior tentorial pits on either side of the epistomal suture. The anterior tentorial arms extend caudally at an oblique angle to the longitudinal axis of the body and terminate in the sides of the postocciput at the occipital foramen (or neuraforamen). The broad, flattened, fused cranial plate of some lower insects is not formed in Mecoptera. Instead, the posterior tentorial arms recess into the postoccipital area and do not project into the foramen. The anterior tentorial arms remain as paired, but not fused, thickened hollow rods that cross the head and form a suspensorium for various organs.

From the middle of the dorsal side of each anterior arm, there is an antero-dorsal process, the dorsal tentorial arm, which extends to the base of the antenna. In those families having a rotator of the scape, the dorsal arm extends up to the base of the antenna, where a portion of the rotator inserts on its apex. Those families lacking a rotator retain the dorsal arm as a shortened projection extending toward the antennal base.

Originating on each tentorial arm near the bases of the dorsal arms are a pair of medial processes which come together but do not fuse. In all Mecoptera (except Panorpidae and Boreidae) these medial processes bear the origins of the tentoriocardinal muscles. That this is primitively so and that the migration of these muscles to a clypeocardinal position (in Panorpidae and Boreidae) is of secondary origin is further supported (aside from being widespread in other Mecoptera) by the fact that in the lower pterygotes these muscles are always tentoriocardinal (Matsuda, 1965).

The tentorium of Mecoptera plays a major role as the internal skeleton of the cranium and serves for the origins of the antennal muscles (Figs. 18-20), the tentoriocardinal muscles (Figs. 11-12), and the tentoriostipital muscles (Figs. 11-12). The medial processes of the anterior tentorial arms are ventrally curved at their apices and form a trough in which the pharynx is situated (the "postpharynx" of Otanes). Although the genaponta is not ontogenetically related to the tentorium, it does serve for the origin of the premental retractors. The tentorium proper is remarkably constant, and its variations are limited to thickness, the extent of arching in the center of the head, the degree of ventral slope in the anterior arms, and the amount of splay from the occipital foramen.

The tentorium of Mecoptera has been previously studied by others: Setty (1940) discussed and illustrated it in Bittacidae; Otanes (1922) in Panorpodidae; Issiki (1933), Heddergott (1938), and Ferris and Rees (1939) in Panorpidae. In general terms my findings confirm theirs. Ferris and Rees made a curious error in their study of Panorpidae when they stated that the only external evidence of the anterior tentorial arms were darkly pigmented spots. In actual fact, the anterior arms of all Mecoptera retain their external openings (anterior pits). The anterior pits are generally subcircular but in Bittacidae are often oblique slits. In *Pazius* (Bittacidae) the pits at first seem absent but they are tucked into recesses beneath the extremely bulging compound eyes.

MANDIBLES

Although the mandibles (mn) are not involved in the elongation of the head into a rostrum, they have undergone certain modifications concomitant with this change. They have become displaced toward the apex of the rostrum and articulate with the head capsule below the level of the other gnathal appendages (Figs. 32, 39, 47). The mandibles attach to the head by a dicondylic articulation consisting of an anterior epicondyle (eci) and a posterior hypocondyle (Fig. 3, hc). The point of articulation varies depending on the ventral extension of the subgena and the length of the rostrum.

Unlike other insect epicondylar articulations, the epicondyle of Mecoptera is retained only as a slight, relatively unsclerotized knob that articulates with a ventrolateral inflection of the clypeus. The more strongly developed hypocondyle articulates in a cavity of the subgena (Fig. 3). The mandibles are decussate in repose, each projecting between the opposite galea and lacinia (Fig. 32). In cross section the mandible is triangular at the base (its relative thickness can be seen in lateral view) but flattens out below the articulation into a tapered blade (Fig. 5).

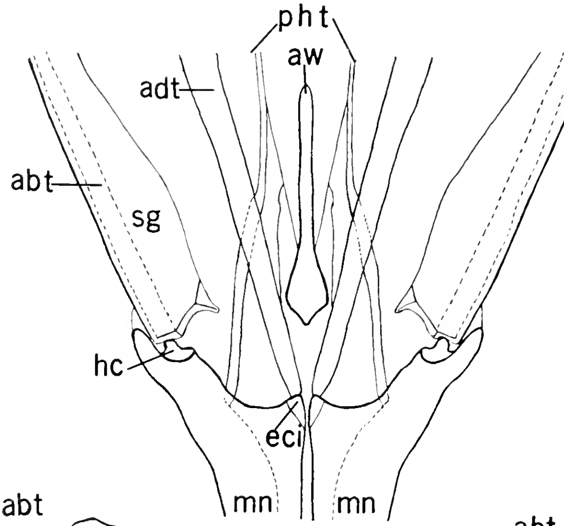
This displacement of the mandible is presumably related to a change in feeding habits, and a partial loss of the normal masticatory function of a chewing mandible has resulted. The mandibles of Mecoptera vary in their width/length ratio and in dental armature on the inner surface of the mandible which is variously toothed. The number of mandibular teeth is constant in each family. Both the mesal and lateral edges of the mandible are more heavily sclerotized than is the flat central plane (Figs. 4, 6). The only Mecoptera with an unusual mandible are the Nannochoristidae, which have very reduced mandibles and lack mandibular tendons.

The apical displacement of the mandibles combined with retention of a generalized musculature has been compensated for by the development of two large apodemes, an abductor (abt) and adductor (adt) tendon for each mandible (Figs. 3-4, 6-7). The muscles that move the mandible insert on the distal ends of these apodemes. The more strongly developed adductor apodeme attaches to a small protuberance on the base of the inner edge of the mandible. It splays above the level of the corporotentorium, providing an extensive area for muscle attachment. The abductor apodeme is well developed but not as extensive as the adductor. The abductor apodeme attaches to the outer edge of the mandibular base in an inflection of the subgenal wall (Fig. 3). It is ventrolateral to the adductor apodeme.

The number of mandibular muscles is inconstant in Mecoptera. The only detailed study of these muscles was of Panorpidae by Heddergott (1938) and I have found that most of the families correspond with his descriptions.

Tergal adductors (Fig. 2, mdm). The adductors are subdivided into three parts by the adductor apodeme, which is T-shaped in cross section; part 1 arises on the vertex; part 2 on the postgena; part 3 is formed by two convergent bands that arise on the gena, postgena, and vertex. Since these bands are divided by the mandibular apodeme, Heddergott (1938) named each band accordingly; but since they function together as a single adductor it is not necessary to formally name each band.

Clypeo-apodemal adductor (Fig. 2, cdm). This muscle is the second mandibular adductor of Heddergott; it arises on the clypeus and inserts directly on the shaft of the mandibular apodeme below the insertion of the tergal adductors. Portions of the muscle arise dorsally on the antennarium and the circumocular sclerite. Heddergott (1938) considered this arrangement to be secondarily derived and that the clypeoapodemal muscles are derived by fragmentation of the tergal adductors. He predicted that in those Mecoptera with a shortened rostrum (Panorpodidae), the clypeoapodemal



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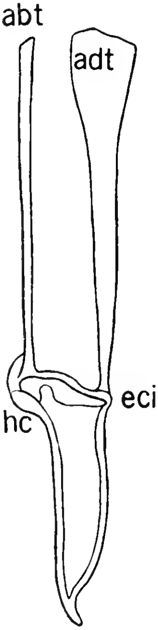

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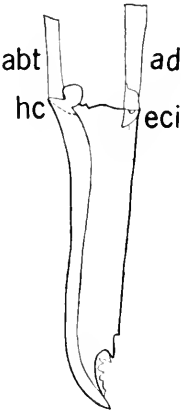

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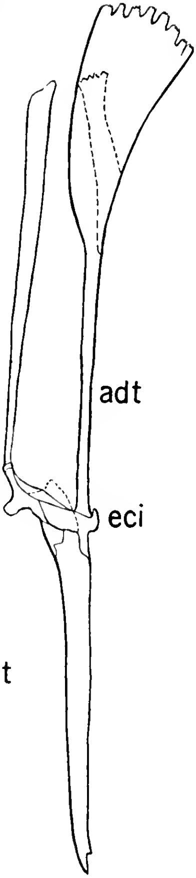

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FIG. 3. *Bittacus chlorostigma.* Caudal view of mandibular complex after labium and maxillae have been removed. Note complexity of skeletal elements and the Apodemalwalze (aw) and status of the articulations of the mandibles.

FIG. 4. *Chorista australis.* Mandible with tendons and condyles.

FIG. 5. *Notiothauma reedi.* Lateral view of articulation of mandible with rostrum.

FIG. 6. *Notiothauma reedi.* Lateral view of mandible with tendons and condyles.

FIG. 7. *Bittacus chlorostigma.* Lateral view of mandible with tendons and condyles.

muscles would be greatly reduced and perhaps reunited with the tergal adductors. I have found this the case in Panorpodidae.

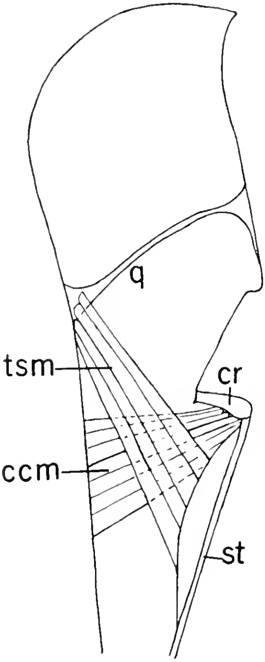
Tergal abductor (Fig. 2, mbm). This muscle is the antagonist of the adductors and is ventrolateral to them. It arises on the gena and vertex and inserts on the abductor apodeme. The abductor is not subdivided as are the adductors.

It is difficult to describe a basic plan of mandibular musculature for Mecoptera and to designate portions as secondary. In terms of other Pterygota, the division in Mecoptera of the adductors first into a tergal group which is further subdivided and second into a group of clypeoapodemal muscles should be regarded as a secondary development. The situation is complicated by the fact that there are three possible combinations in Mecoptera. One group (Panorpidae, Panorpodidae, Meropeidae, Apteropanorpidae, Boreidae and probably Choristidae although none could be checked) possesses the full set of tergal and clypeoapodemal adductors and abductors. This group also contains rostra of all three lengths. A second group contains Bittacidae and Notiothaumidae in which there are no clypeoapodemal adductors. The other muscles are present and well developed, as in the first group. Heddergott (1938) indicated a similarity between Bittacidae and the nematocerous Diptera. A third group contains Nannochoristidae, which completely lacks mandibular apodemes. I have been unable to find any trace of a mandibular musculature in this family, and the conclusion that the mandibles are functionless was previously advanced by Evans (1942).

Because of the nature of the mandibular articulation with the head capsule, the mandibles are almost or wholly limited in their movement to abduction and adduction. Some slight protraction and retraction might possibly occur as well.

MAXILLAE

Although the maxillae participate in the formation of the rostrum by the elongation of their stipites, their structure is typical of that of many pterygote chewing insects. The maxilla (mx) of Mecoptera consists of a cardo (cr), stipes (st), lacinia (lc), usually a galea (gl), and a maxillary palp (mxp) (Figs. 30-32, 34-38, 41). The cardines are approximately triangular sclerites by which the maxillae articulate with the cranium below the postgenal bridge. The stipites are elongate, their length varying with the length of the rostrum. The maxillary palps are five segmented in all Mecoptera and arise at the apex of the stipites by membranous palpifers. The stipes bears two apical lobes, an inner lacinia and an outer galea. These lobes vary in their dimensions and degree of basal fusion, and in Nannochoristidae one of the lobes (the galea) is absent. When both lobes are present (Fig. 9), there is an apodemal framework consisting of two heavily



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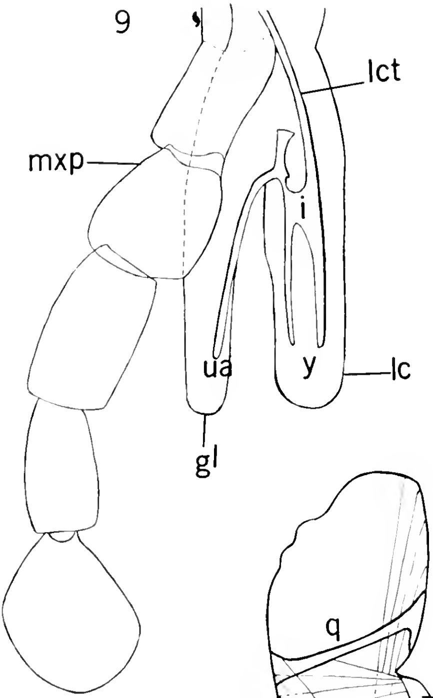

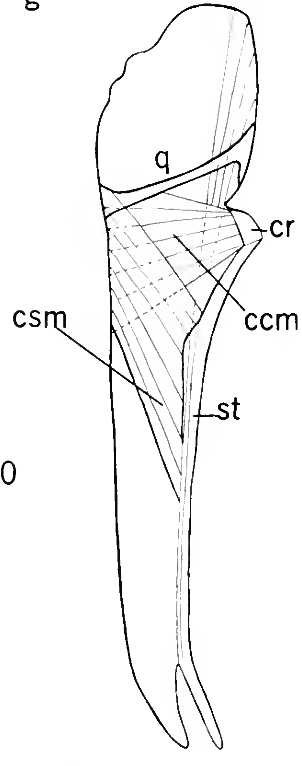

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FIG. 8. *Boreus* sp. Longitudinal section of head with extrinsic effectors of the maxilla. Note clypeocardinal muscle.

FIG. 9. *Chorista australis*. Maxilla with its internal apodemal framework.

FIG. 10. *Panorpa nuptialis*. Longitudinal section of head with extrinsic effectors of the maxilla. Note that both muscles are clypeal rather than tentorial in origin.

sclerotized rod-like processes (y) in the lacinia and one in the galea (ua), all of which are basally fused. The outer process of the lacinia continues dorsally as an elongate lacinial tendon (lct) on which the tergolacinial muscles (tlm) insert at the level of the posterior tentorial arms. This tendon or apodeme is characteristic of the maxillae of all Mecoptera regardless of the degree of development of the galeal and lacinial processes or whether the galea is present or not. The tendon varies with the length of the stipes.

The major skeletal variation in the maxilla involves the lacinia and galea. Because of the extreme degree of fusion of these parts in Panorpidae, and the absence of the galea in Nannochoristidae, there has been general disagreement over the correct interpretation of these parts. By superficial comparison with Diptera, Otanes (1922) regarded the lacinia as suppressed, with the result that the two lobes represent a subdivided galea. Issiki (1933) agreed with this interpretation. Heddergott (1938) rejected the former view in favor of the one described above. The most convincing arguments for the interpretation of these parts as presented here are in the comparative study by Imms (1944). On the basis of musculature, Imms concluded that the inner lobe is, in fact, the lacinia and the outer lobe, when present, the galea. I concur with this view.

There is a graded series in the development of the galea and lacinia from well developed and separated lobes in Bittacidae to the absence of the galea in Nannochoristidae. Between these endpoints, the variations are of three kinds. In Notiothaumidae, Meropeidae, and Apteropanorpidae, the galea and lacinia are quite distinct and are fused only at the apex of the stipes. In Choristidae, Panorpodidae, and Boreidae, both lobes are shorter than those in the preceding group and there is more fusion of the lobes. Lastly, the Panorpidae are unique in that both lobes are present but reduced in size and are completely continuous with the stipes, forming a single piece. The galea and lacinia of Mecoptera are characteristically covered with a variety of spines and setae, some of which form a conspicuous brush on the apex of the lacinia as in Meropeidae (Figs. 35, 42). The anatomical details of these setae are well illustrated for Panorpidae by Heddergott (1938) and for other families by Otanes (1922).

The maxillary musculature of Mecoptera is more variable than that of either the mandible or labium, but there is a basic plan which consists of the following elements:

Tentoriocardinal muscles (Figs. 11-12, tcm). These muscles arise on the medial tentorial process and insert on the cardo. They are perpendicular to the long axis of the head (parallel to the longitudinal axis of the body) and are adductors or depressors of the maxillae.

Tentoriostipital muscles (Figs. 1, 8, 11-12, tsm). These muscles arise on the medial tentorial process (anterior to the tentoriocardinals) and on a portion of the anterior tentorial arms and extend obliquely to the stipes, where they insert on both sides of the stipital process. There are two distinct tentoriostipital muscles. The first and more dorsal muscle is the abductor and is antagonistic to the tentoriocardinal muscle. The second (often termed the stipital promotor) is like the first except that its insertion is below that of the first and is consequently more obliquely oriented. This muscle is the promotor of the stipes and those parts below the stipes. In some families these two muscles often appear continuous; in others, they are distinctly separated.

Tergolacinial muscles (Figs. 11-13, tlm). These muscles arise as two distinct groups, an anterior occipital and a posterior postgenal group, and insert on the maxillary apodeme (an extension of the base of the lacinia). The two muscles function as one flexor of the lacinia (which is the cranial flexor of most other insects).

Stipitopalpal muscles (Fig. 11, spm). These muscles are the extensors of the palp. They arise near the base of the stipes and insert on the first segment of the palp.

Palpal muscles. The first of these is the second extensor of the palp and arises in the first segment and inserts in the second segment. This muscle is followed by flexors in the third and fourth segments of the palp.

The maxillary musculature as outlined above occurs in Panorpodidae, Bittacidae, Meropeidae, Notiothaumidae, Apteropanorpidae, Nannochoristidae, and probably Choristidae, though none were checked. The two exceptions to the above scheme are Panorpidae (Fig. 10) and Boreidae (Fig. 8). This is unfortunate because most of the generalizations that have been made about Mecoptera and passed on in the textbooks are based on studies of Panorpidae by Issiki (1933), Hetrick (1935), and Heddergott (1938) and do not reflect the condition of Mecoptera as an order. Panorpidae deviates from the general scheme in two respects. The tentoriocardinal muscles of other Mecoptera are clypeocardinal in Panorpidae and both groups of tentoriostipitals of other Mecoptera are clypeostipital muscles (csm) in Panorpidae. Although these three muscles have shifted their origins in Panorpidae, they function as do their counterparts in other Mecoptera. The interpretation of the condition in Panorpidae as secondary is further supported by the situation in Boreidae. The Boreidae are intermediate between the majority of Mecoptera and Panorpidae. In Boreidae the "tentoriocardinal muscles" are clypeocardinal (as in Panorpidae), but the tentoriostipitals are extremely oblique and some of the fibers arise on the tentorium (as in most Mecoptera) while others arise on the clypeus. Matsuda (1965) claimed that the secondary development of the tentoriocardinal muscles migrating to a clypeocardinal position is correlated with the elongation of

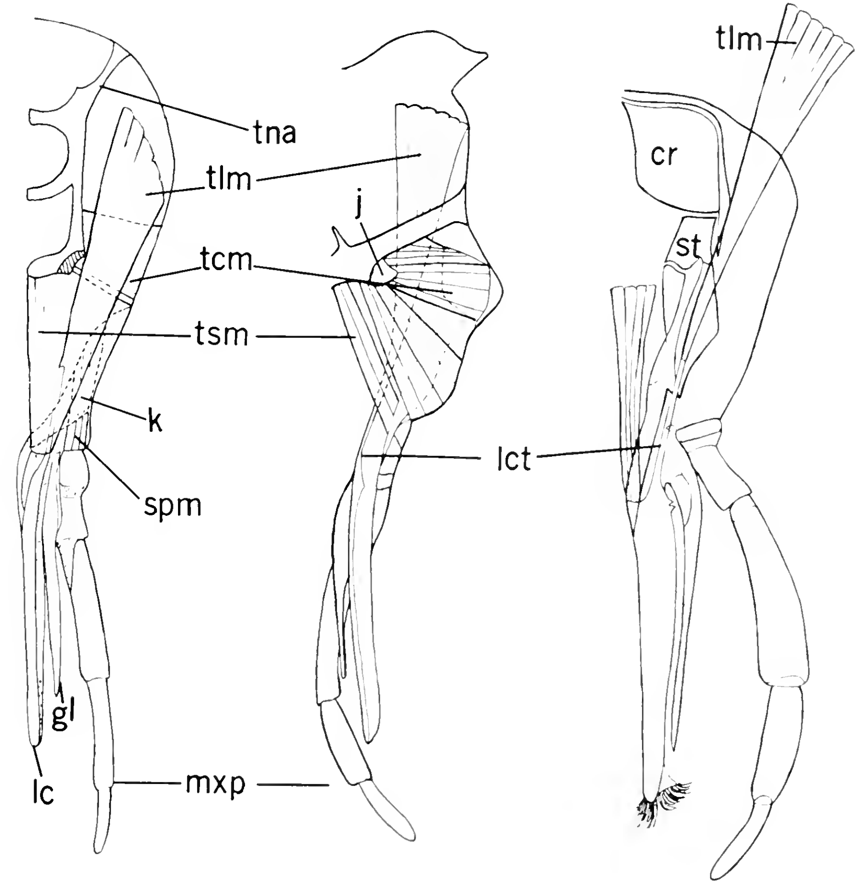

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FIG. 11. *Bittacus chlorostigma*. Anterior view of maxilla and its muscles. Note that most of the extrinsic effectors are tentorial in origin.

FIG. 12. *Bittacus chlorostigma*. Lateral view of same.

FIG. 13. *Bittacus chlorostigma*. Anterior view of same with tsm and tcm muscles removed.

the rostrum, as in Panorpidae and Boreidae. This conclusion is tenuous at best since there is no constant proportional difference in the relative distance of the tentorium from the apex of the rostrum in tentoriocardinal families and clypeocardinal families. Some of the tentoriocardinal families (Bittacidae, Notiothaumidae) have a greater distance between tentorium and the apex of the rostrum than does the clypeocardinal family Boreidae. The Panorpidae do, however, exhibit the greatest distance between the tentorium and the apex of the rostrum.

LABIUM

The labium of Mecoptera is composed of two parts, a proximal postmentum and a distal prementum (Figs. 30-38). The postmentum (pk) varies in extent and degree of sclerotization. In most Mecoptera the postmentum is membranous and has a distal mental plate (mp). The exceptions are Meropeidae (Fig. 35) and Nannochoristidae (Fig. 31) in which the postmentum is entirely membranous, the Boreidae in which it is completely fused into a single sclerite (zygostipes of Crampton, 1942) accompanied by the mesal fusion of the maxillary stipites (Fig. 30, mlc), and lastly the Nannochoristidae in which it is greatly reduced. It lies between the maxillary cardines and stipites and is separated from the foramen magnum by a postgenal or hypostomal bridge (pgb, hyb). The prementum (rk) is usually sclerotized and may extend over the base of the labial palps. The labium and maxillae are laterally fused and form the posterior wall of the rostrum. The prementum bears two membranous palpifers, each bearing a two segmented labial palp (lp). The mesal line of fusion between the presumably once separated lobes of the prementum is visible in all Mecoptera, although it has become slightly obliterated in Panorpodidae. There is no remnant of a ligular structure in any Mecoptera.

The base of the postmentum is always fused with the maxillary cardines and stipites but the extent of the lateral fusion varies. In Notiothaumidae, Choristidae, Panorpidae, and Apteropanorpidae the line of fusion extends to the base of the mental plate. In the remaining families the line of fusion extends below the mental plate to the base of the prementum.

The position and configuration of the mental plate is variable in Mecoptera but it is generally quadrate except in Bittacidae, where it is extremely narrow and elongate (Figs. 32-33). The prementum is likewise variable. The premental lobes of Choristidae are separated at their apices but fused at their bases with a discernible fusion line (Fig. 37). According to Bierbrodt (1942) both the larva and pupa of Panorpidae have a three-segmented palp, which is reduced to two segments in the adult. Presumably this holds for the other families as well. The basalmost segment of the preimaginal palp becomes the palpiger of the adult palp. The palpiger is reduced and continuous with the apex of the prementum and bears the base of the palp. It varies in size and is completely absent in Bittacidae.

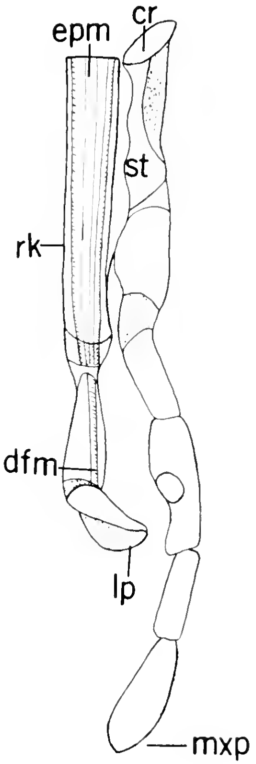
There are four possible sets of muscles that operate the labium of Mecoptera:

Retractors of the prementum (rnm). These are paired muscles on either side of the labium that arise on the ventral edge of the postgenal bridge and insert either a) directly on the base of the prementum (Fig. 16), or b) on an apodeme (ra) which extends dorsally from the base of the prementum (Figs. 15, 17).

Extensors of the labial palp (epm). These muscles arise either on a) the base of the prementum (Figs. 16-17), or b) the retractor apodeme (Fig. 15). In both instances the muscles insert on the base of the first segment of the palp (Figs. 15-17).

Flexors of the palp (fpm). These muscles arise on the mesal line of fusion of the prementum and insert on the base of the first segment of the palp.

Distal flexors of the palp (dfm). These muscles arise on the base of the first segment and insert on the base of the second (Figs. 14-17).



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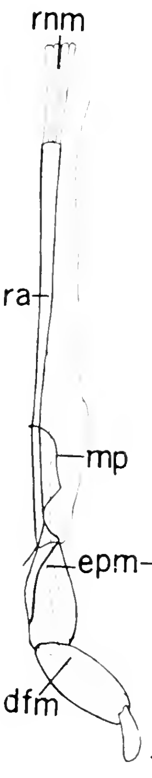

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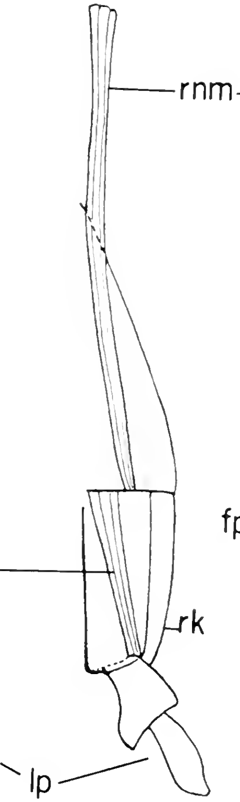

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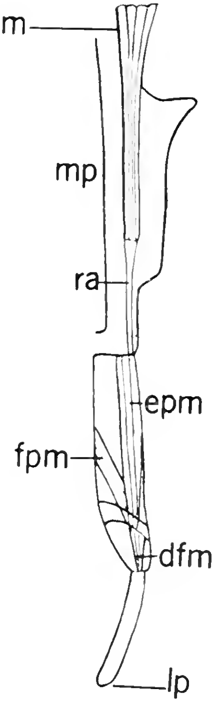

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FIG. 14. *Nannochorista dipteroides.* Caudal view of labium and maxilla. Note absence of rnm and fpm muscles.

FIG. 15. *Panorpa nuptialis.* Caudal view of labium. Note absence of fpm muscle and origin of epm muscle on tendon (ra).

FIG. 16. *Merope tuber.* Caudal view of labium. Note absence of tendon and fpm muscle.

FIG. 17. *Bittacus chlorostigma.* Caudal view of labium. Note presence of fpm muscle which is unique to the Bittacidae.

Only the Bittacidae possess all four of these muscle sets, and in addition they possess well developed retractor apodemes (Fig. 17). Nannochoristidae (Fig. 14) and Boreidae lack both a premental retractor and a flexor of the first segment of the palp. In the remaining families there is a premental retractor, an extensor of the first segment of the palp, and, according to Imms (1944), a flexor of the second segment of the palp. These families lack a flexor of the first segment of the palp. The relative lengths of these muscles and of the retractor apodeme naturally vary with the development of the rostrum. The retractor apodeme is notably long in Panorpidae with a consequently shortened premental retractor. There is no retractor apodeme or flexor of the second segment of the palp in Meropeidae and Notiothaumidae.

There has been much confusion about the labium of Mecoptera, most of which stems from old controversies about the nature of the insect labium in general. Otanes (1922), for example, interpreted the apex of the prementum as a fusion product of former ligular components, imagined that it was unique to Mecoptera, and termed it the mecaglossa. Although there is no trace of ligular remnants (stipulae, glossae, paraglossae) in Mecoptera, there is no basis for this interpretation. Otanes also stated that the palpigers are also part of this fusion product, which is incorrect (as shown by Bierbrodt, 1942). Subsequently there was a long controversy between Crampton and MacGillivray over the interpretation of the labium that did not resolve the problem. In his study of the labium of Holometabola, Crampton (1925) illustrated and discussed the labium of Bittacidae, Panorpidae, Choristidae, and Nannochoristidae but confused the postmentum with the mentum and the prementum with the palpiger. Issiki (1933) and Heddergott (1938) followed a different interpretation in which they designated the postmentum as the submentum in Panorpidae and Panorpodidae. This interpretation is unacceptable since the mental plate occurs alone without a separate sclerotized submental plate. There is no basis for the recognition of a submentum as such and the single plate of the postmentum should be designated as the mental plate to be consistent with the generalized insect labium (Snodgrass, 1935). Setty (1940) interpreted these structures correctly in his study of Bittacidae.

The greatest difficulties in the interpretation of the labium of Mecoptera attend the Nannochoristidae. In a study of this family, Evans (1942) dispelled the notion of a gula in Nannochoristidae (an interpretation retained by Matsuda, 1965) but misinterpreted the components of the labium. Evans stated that the prementum is reduced to a narrow membranous band confluent with the palpigers and that the single sclerite of the postmentum represents the mentum (which is actually the prementum). In an otherwise fine comparative study of the labium of Mecoptera and Diptera, Imms

(1944), apparently unaware of Evans' paper, offered yet another interpretation of the labium in Nannochoristidae. He stated that: 1) there is a gula which separates the occipital foramen from the postmentum; 2) that the retractors of the prementum arise on the apex of the gula; 3) that the premental lobes are completely separated; 4) that the flexor muscles of the second segment of the palp arise on the base of the prementum; and 5) that the labial palps of all Mecoptera are two segmented. He incorrectly criticized Tillyard (1917) and Crampton (1921) for having designated the prementum as the first segment of the labial palp and attempted to support this claim with evidence from musculature (since the muscles of the labial palps arise from the prementum and labial retractors insert on its base).

Imms' interpretation is rejected on the basis of the following general criteria, based mostly on Snodgrass (1935) and Matsuda (1965). The prementum is defined and identified by the presence of the retractors on its base. The postmentum should be termed the submentum if it includes a distinct mental plate. A correct interpretation of Nannochoristidae is difficult because 1) the postoccipital sutures partially extend into the postgenal bridge (creating the illusion of a gula where there is none), 2) there is no retractor of the prementum, 3) the postmentum is greatly reduced. The similarities which Imms sought between Mecoptera and Diptera also involved a misinterpretation of the labium in certain nematocerous Diptera. Wenk (1962) showed that the postmentum of some Nematocera is often greatly reduced and that the postgenal processes are simultaneously well developed, a situation identical to that in Nannochoristidae. What Imms illustrated and termed the postmentum still retains the mesal line of fusion (as in all other Mecoptera) between once separated lobes; however, the postmentum of an insect labium never exhibits a trace of a fusion line anywhere. It is the prementum which has the median fusion line. The actual postmentum of Nannochoristidae is greatly reduced. Likewise, it is impossible to claim a two-segmented labial palp (as Imms tried) if his designations are accepted, because this interpretation would leave only one segment for the palp. This same observation was made by Hoyt (1952) in his study of the evolution of the head and mouthparts of Diptera. The Nannochoristidae (Figs. 14, 31) are unusual in that they lack the normal labial retractors and a well defined postmentum. In other respects they conform to usual mecopteran labial structure and have a prementum, a small palpiger, two-segmented labial palps, an extensor of the first segment of the palp, and a flexor of the second segment of the palp.

ANTENNAE

The antennae of Mecoptera (Figs. 18-29) are of the flagellar type characteristic of the Pterygota (Snodgrass, 1928; Imms, 1939; Schneider, 1964;

Matsuda, 1965). Each antenna consists of three parts, two basal musculated segments—a proximal scape (sc) and a distal pedicel (pe)—and a flagellum consisting of a varying number of flagellomeres, none of which is musculated. The antennae are connected to the head capsule in the frontal area between the compound eyes (co) and below the ocelli (oi) by an extensive membranous socket, the antacorium (act). The antennal base and the antacorium are circumscribed by the antennal sclerite or antennarium (aj), which is reinforced by an internal submarginal ridge, the antennal suture (ans). The antennarium bears a ventrolateral antennifer (anf) which functions as the single pivotal point of articulation for the base of the scape with the head capsule.

In Mecoptera, as in other Pterygota, movement of the antenna is effected by extrinsic muscles which arise on the dorsal side of the anterior tentorial arms and insert on the base of the scape. The general pterygote antennal musculature consists of 1 or 2 pairs of levators and 1 or 2 pairs of depressors of the scape (Snodgrass, 1928; Imms, 1939; Schneider, 1964; Matsuda, 1965). There is a single pair of levators and depressors for each antenna of Mecoptera. Heddergott (1938) worked out the basic structure in Panorpidae; Setty (1940), the Bittacidae; and I have corroborated their findings and also examined the other families. The basic pattern is as follows:

Depressor muscles of the scape (dsm). The depressors of the scape arise on the dorsal surface on the anterior tentorial arms (q) and insert on the ventral basal rim of the scape (Figs. 18-20). The attachment is off-center and simultaneously depresses the antenna and turns it slightly to the outside.

Levator muscles of the scape (lsm). The levators arise just behind the depressors at the point of origin of the dorsal tentorial arms (v) and insert on the dorsal edge of the base of the scape (Figs. 18-20). Being thus obliquely oriented, they simultaneously raise the antennae and rotate them medially.

Rotator muscles of the scape (rsm). In some Mecoptera there is an unusual muscle, the rotator of the scape, which arises either on the frons or the dorsal tentorial arm and inserts on the dorsolateral side of the antacorium. In those families in which the muscle arises on the frons, the dorsal tentorial arm continues up to and terminates on this muscle. Because of its oblique course, it rotates the scape mesally and might contribute slightly to the elevation of the whole antenna.

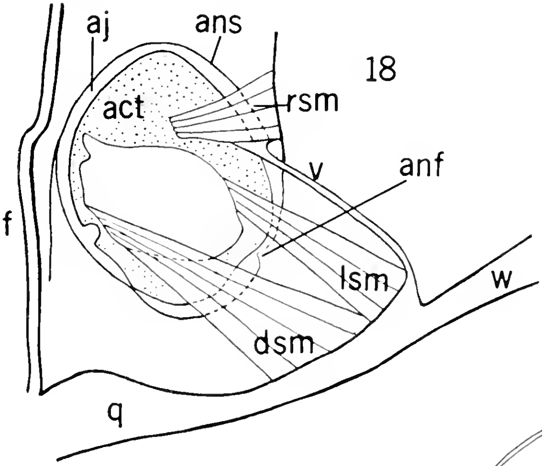
The intrinsic muscles of the antennae are those that arise on the base of the scape and insert on the base of the pedicel.

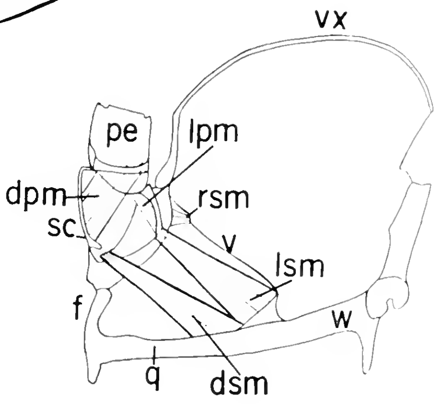
Levator muscles of the pedicel (lpm). The levators of the pedicel arise on a reinforced ridge that circumscribes the base of the scape and insert on the base of the pedicel (Figs. 19-20).

Depressor muscles of the pedicel (dpm). The depressors of the pedicel are situated opposite the levators and function antagonistically to them

(Figs. 19-20). The relative size of the levators and depressors varies but the depressor is usually the larger of the two.

The flagellomeres are only passively movable with respect to one another and the basal segments. With the exception of the rotators of the scape, all





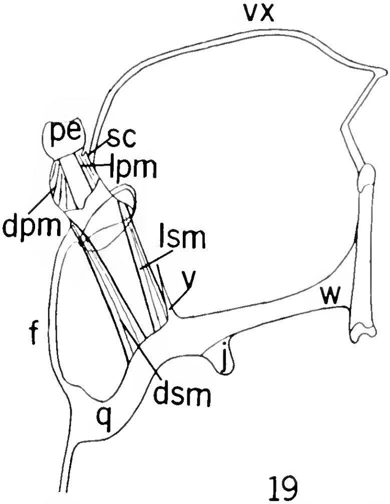


Fig. 18. *Panorpa nuptialis*. Three-quarters profile of longitudinal section of right antennal connection with the head. Note the disposition of the antenniferal pivot (anf) as well as the peculiar rotator of the scape (rsm).

Fig. 19. *Bittacus chlorostigma*. Longitudinal section of antennal connection with head. Note the absence of rsm.

Fig. 20. *Panorpa nuptialis*. Longitudinal section of antennal connection with head. Note rsm and the oblique placement of dm and lpm.

families fit the above description. A rotator of the scape ocurs in Panorpidae, Panorpodidae, Apteropanorpidae, Meropeidae, and Notiothaumidae but not in the other families.

There are slight variations in the external morphology of the antennae that involve the antennifer, antacorium, antennarium, antennal suture, and the number and shape of the flagellomeres. An antennifer is present in all families of Mecoptera except the Bittacidae. Although the extent of the antacorium varies, it is generally more extensive in Mecoptera than in other insects. An antennarium is present in all Mecoptera and is most extensive in Nannochoristidae; it is unusual in Boreidae inasmuch as it is ventrolaterally incised. In general, the circumantennal suture is well developed and conspicuous in Mecoptera, excepting Panorpidae, in which it is evanescent. The scape is usually obliquely compressed and the pedicel subcylindrical. The flagellum is filiform with the exception of Meropeidae in which it is moniliform. The number of flagellomeres is inconstant both in individuals and in species (Miyake, 1913).

The number of muscles that effect the scape is usually two or four. Since there are only two in Mecoptera, plus the rotator, there are two possible explanations for the origin of the rotator of the scape. It might be regarded as derived from one of the dorsal effectors, with the loss of its ventral antagonist, or as having resulted from enlargement and subsequent splitting of the levator of the scape. The second alternative seems more feasible and would involve fewer developmental modifications to effect this change, as evidenced from various experimental work on insect muscle (Matsuda, 1965).

DISCUSSION AND CONCLUSIONS

Most of the generalizations made about Mecoptera are compared with what is known about other insect orders and about departures from what might have been expected on the basis of a general plan of insect anatomy. Most of the comparative information is taken from Matsuda (1965), who has covered the literature on the insect head thoroughly.

1. In the process of rostrum formation, the relationship between the gena and the clypeus has changed so that the subgena is ventrally displaced along the lateral margin of the clypeus and is posteriorly involuted, forming an articulation for the hypocondylar process of the mandible. The line of fusion between the now extended subgena and the clypeus results in the formation of the clypeogenal suture. A similar formation has occurred in Hymenoptera but not to the same extent as in Mecoptera.

2. The suppression of cranial sutures is not unique to Mecoptera, but progresses from the exopterygotes through the holometabolous orders. A consequence of this trend is the indefinability of cranial regions. The post-

occipital region has moved dorsally and cephalad, as has the occipital region which is fused with the vertex. There is no separation of vertex and genae, hence no distinct parietals. The occurrence of a temporal suture is basic to the Panorpoid Complex but occurs only sporadically among lower pterygotes.

3. The maxillae are generalized and typical of chewing insects. The cardo and stipes are unremarkable except for the formation of a zygostipes (Crampton, 1942) in Boreidae. There has been a trend toward reduction of the galea and lacinia in Mecoptera and in the other Panorpoid orders. The tentoriocardinal and tentoriostipital muscles of Mecoptera (though often absent in higher orders) are modified only in Boreidae and Panorpidae through a secondary shifting of their insertions. The tergolacinial muscles are unusual in that they arise as two bundles and jointly insert on a common lacinial apodeme. The retention of stipitopalpal muscles must be regarded as unusual since they do not occur in other Panorpoid orders. In terms of the theoretically maximum number of maxillary muscles, the tendency in Mecoptera has been reduction in the total number of muscles and the retention of primitive sites of origin and insertion of those retained. Other common maxillary muscles such as tergocardinal, tergostipital, stipitolacinial, and stipitogaleal, while present in lower orders, generally do not occur in the Panorpoid Complex and are completely absent from Mecoptera.

4. The mandibles of Mecoptera vary from extremely reduced to elongate well developed appendages. Their articulations are modified by a close association of the hypocondyle with the subgenal wall and the reduction of the epicondyle and its close association with the Apodemalwalze, which is unique to Mecoptera. It is generally held that the shape of the mandible is directly related to feeding. While this may be so, not enough is known about the feeding habits of Mecoptera to test the assumption. The mandibular muscles show the same tendency toward reduction as do those of other pterygotes and there is nothing unique about these muscles in Mecoptera.

5. The labium of Mecoptera exhibits a combination of primitive characters plus certain losses not usually associated with a primitive state. There is no gula in Mecoptera but the postgenal bridge is well developed and results in a reduction of the base of the labium. The retention of an entirely membranous postmentum and a sclerotized mental plate is regarded as secondarily derived. The complete absence of ligular elements is basic to the Panorpoid Complex. The labial musculature is variable in Mecoptera as it is in other Panorpoid orders. The overall tendency is toward reduction in the number of muscles.

6. A hypopharynx is present in all Mecoptera and is intimately associated with the labium and the pharyngeal trough. Of a half dozen possible hypopharyngeal muscles in insects, none occur in Mecoptera. It is difficult

to generalize about this organ since it is so variable and there is no apparent overall trend in insects.

7. The antennae of Mecoptera are unique only in the possession by some families of a rotator muscle of the scape. Compared to other insects, the antacorium of Mecoptera is extensive.

8. Of the five tentorial elements, only the corporotentorium is variable in Mecoptera, occurring in about half of the families. In lower Pterygota there is a tendency toward fusion of the anterior and posterior arms into a single plate, while the reverse occurs in the higher Pterygota. Mecoptera are somewhat intermediate in this regard since they have a complete fusion of the anterior and posterior arms on either side but no mesal fusion into a single plate. The development of the tentorium in other Panorpoid orders is variable and does not show any particular trend.

9. The modifications of the mecopteran head compared to a generalized head have been twofold: 1) reduction of elements through specialization into a new kind of sucking organ; 2) the retention of many primitive features. All of the structural elements present can be homologized with similar structures in other groups. The modifications discussed have generally been simply the elongation of previously existing structures without change of the basic form of the element concerned, or in some cases reduction and suppression of these elements.

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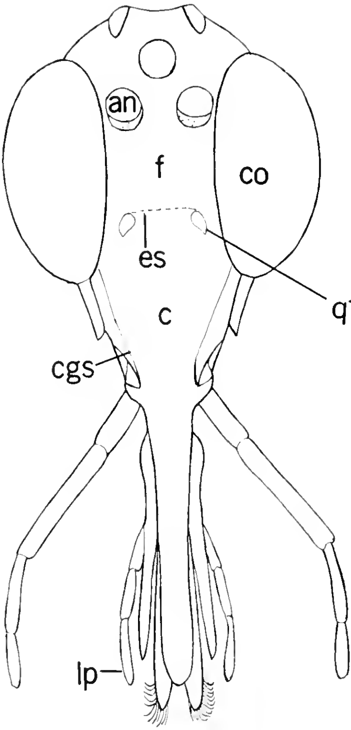

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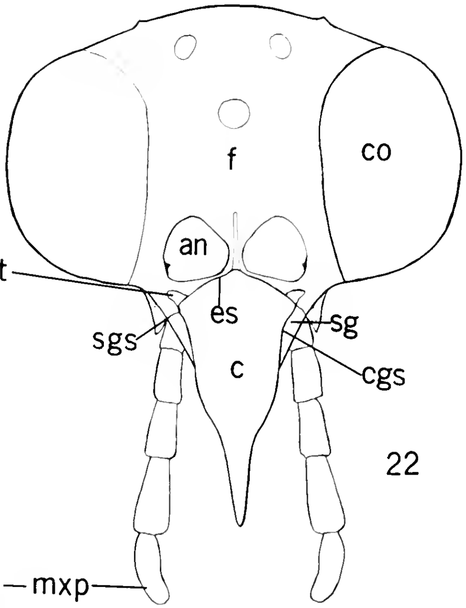

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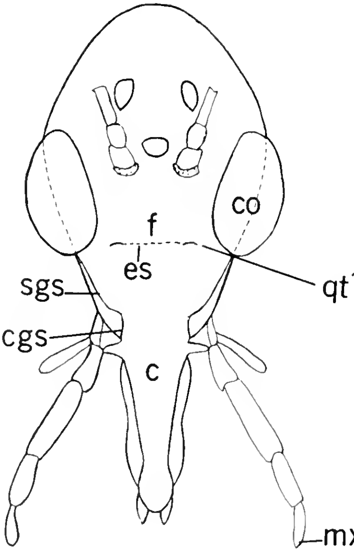

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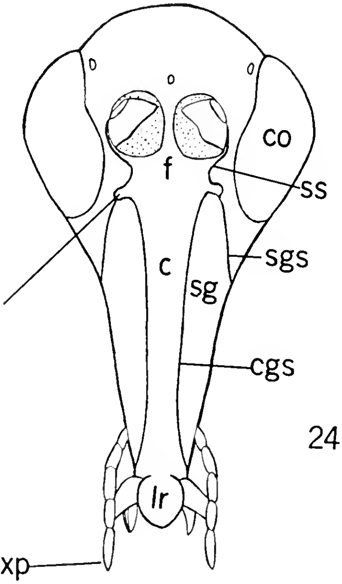

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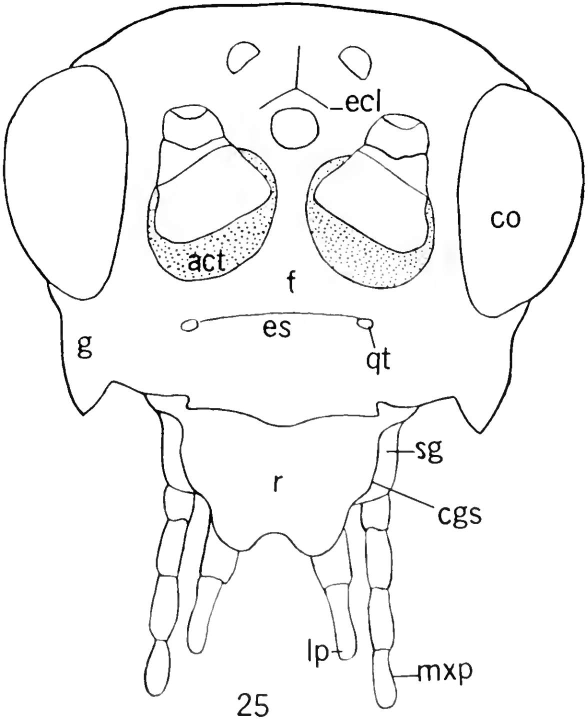
FIG. 21. *Neobittacus blancheti.* Anterior view of head. FIG. 22. *Nannochorista dipteroides.* Same. FIG. 23. *Apterobittacus apterus.* Same. FIG. 24. *Boreus unicolor.* Same.



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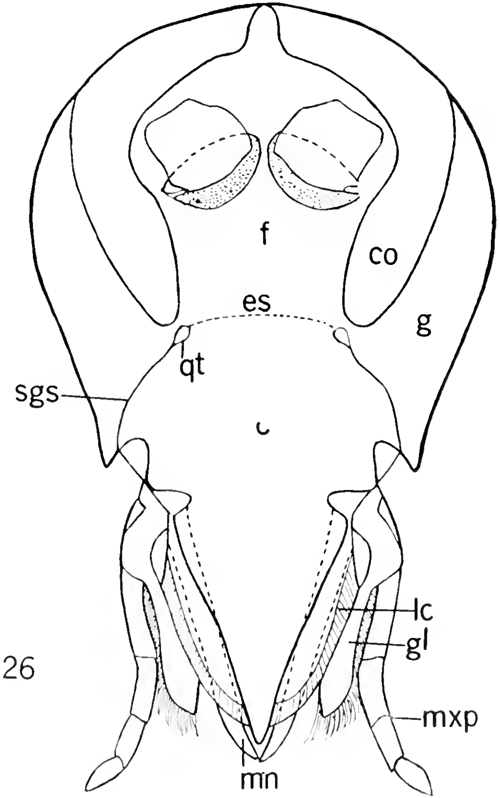

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FIG. 25. *Brachypanorpa carolinensis.* Anterior view of head. FIG. 26. *Merope tuber.* Same.

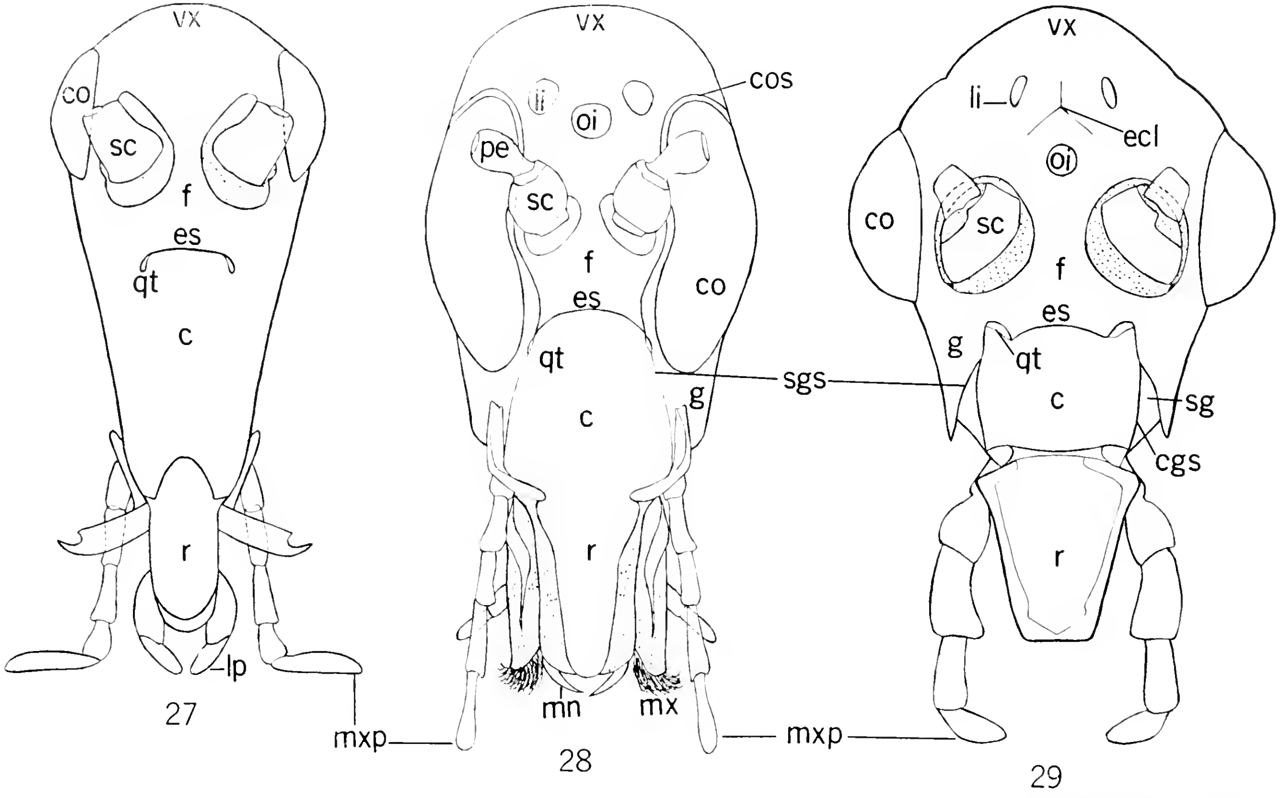
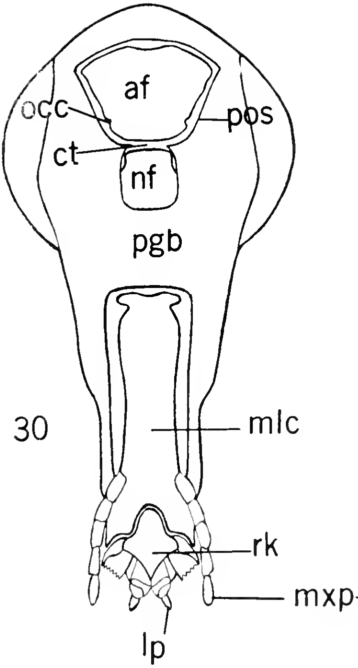


FIG. 27. *Apteropanorpa tasmanica.* Anterior view of head. FIG. 28. *Notiothauma reedi.* Same. FIG. 29. *Chorista australis.* Same.



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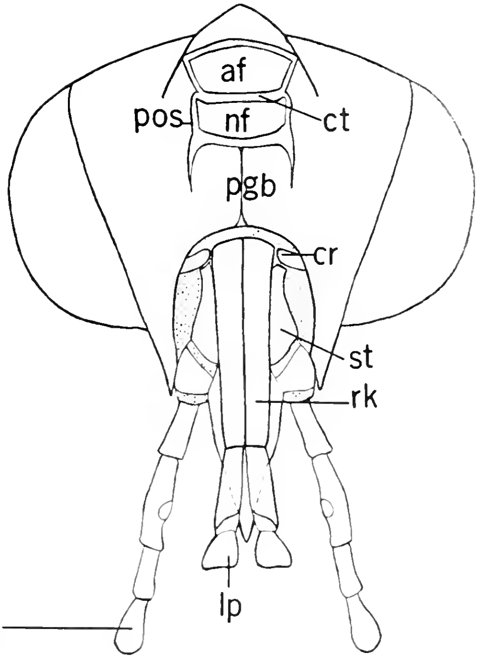

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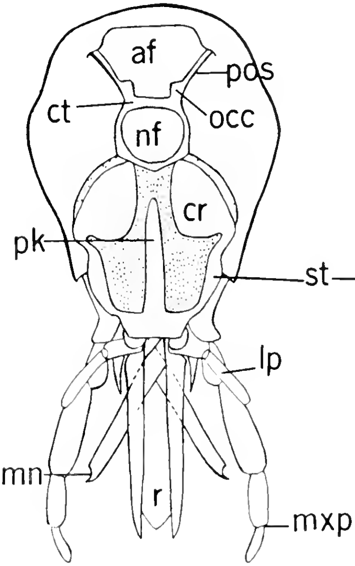

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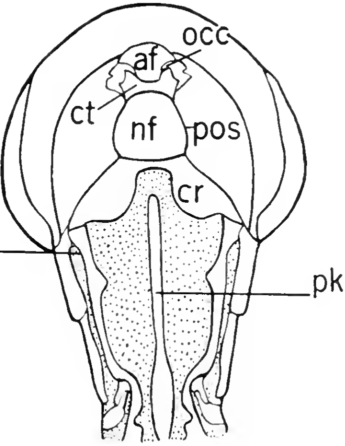

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Fig. 30. *Boreus unicolor.* Caudal view. Fig. 31. *Nannochorista dipteroides.* Same. Fig. 32. *Apterobittacus apterus.* Same. Fig. 33. *Harpobittacus tillyardi.* Same.

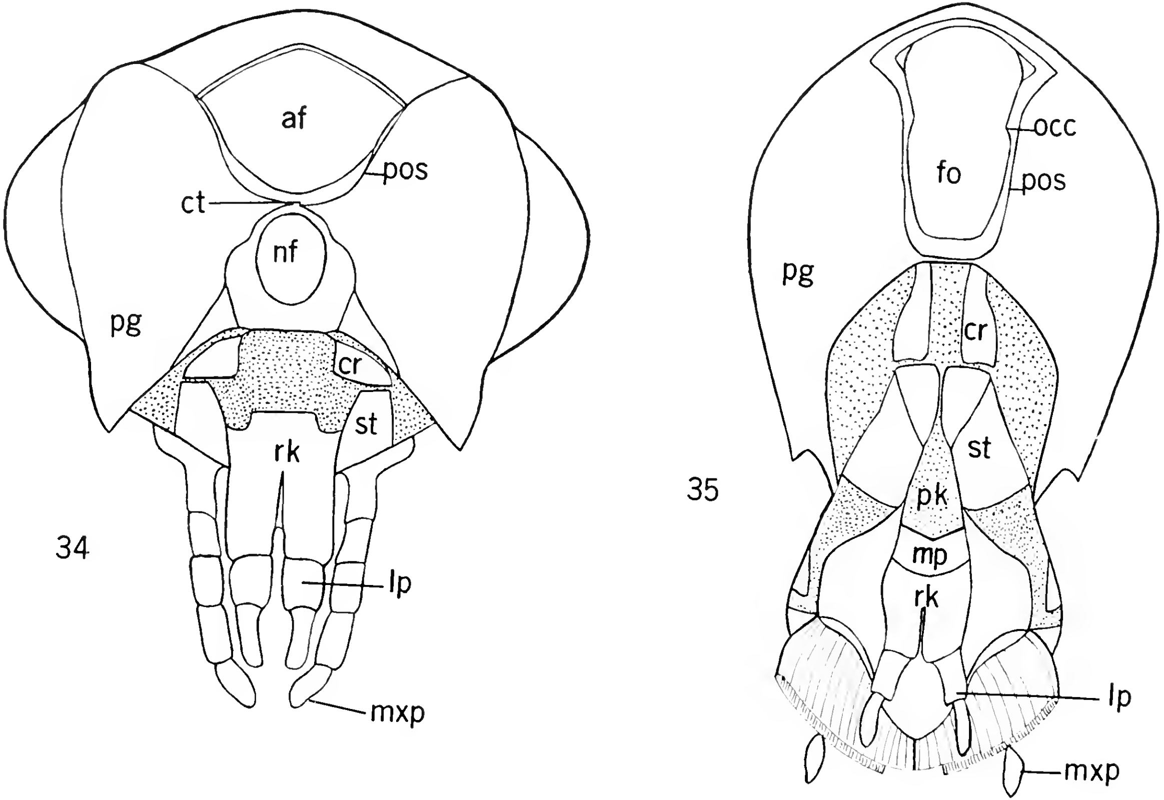
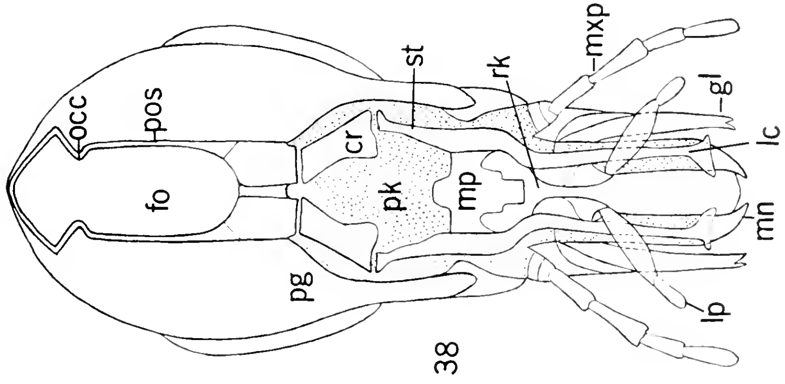


FIG. 34. *Brachypanorpa carolinensis.* Caudal view. FIG. 35. *Merope tuber.* Same.



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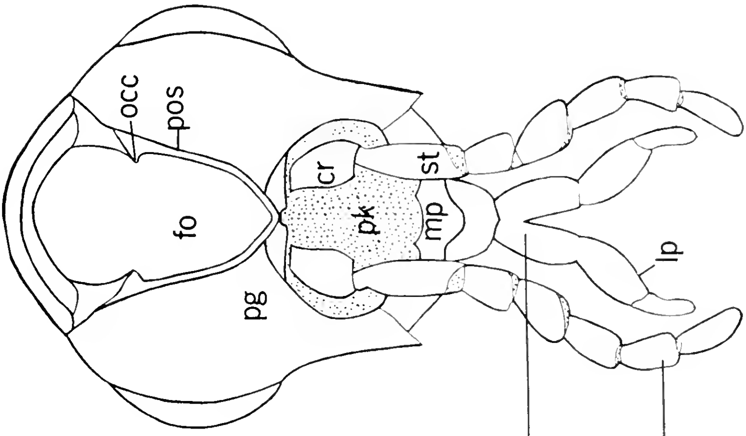

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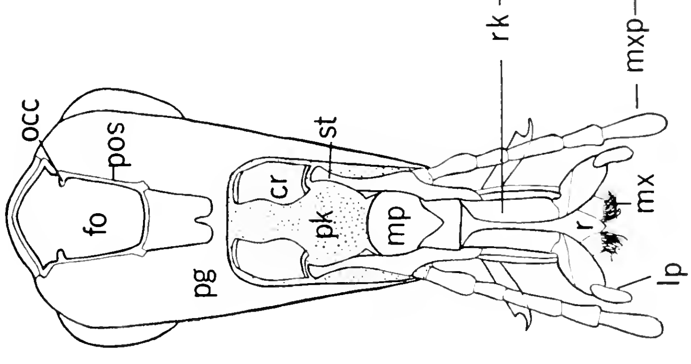

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FIG. 36. *Apteropanorpa tasmanica.* Caudal view. FIG. 37. *Chorista australis.* Same. FIG. 38. *Notiothauma reedi.* Same.

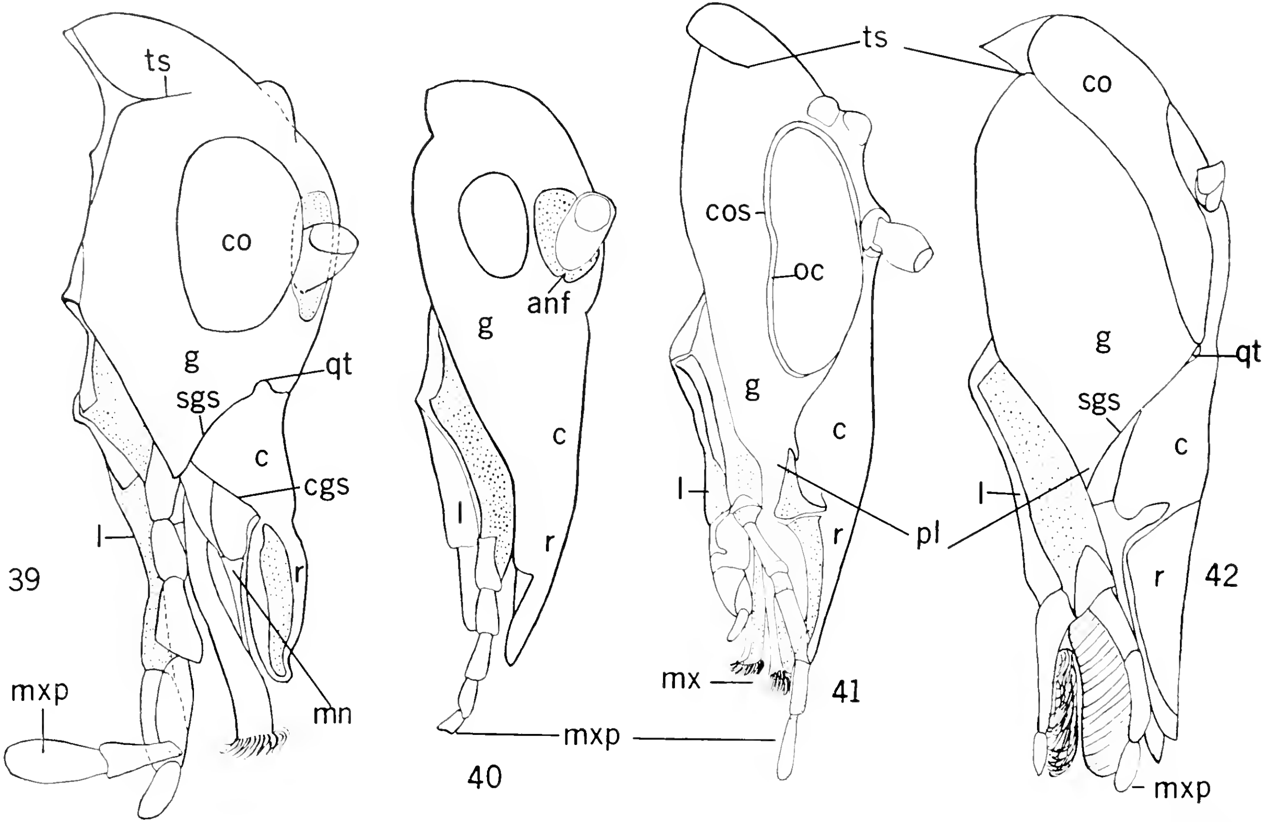

FIG. 39. *Chorista australis.* Lateral view. FIG. 40. *Apteropanorpa tasmanica.* Same. FIG. 41. *Notiothauma reedi.* Same. FIG. 42. *Merope tuber.* Same.

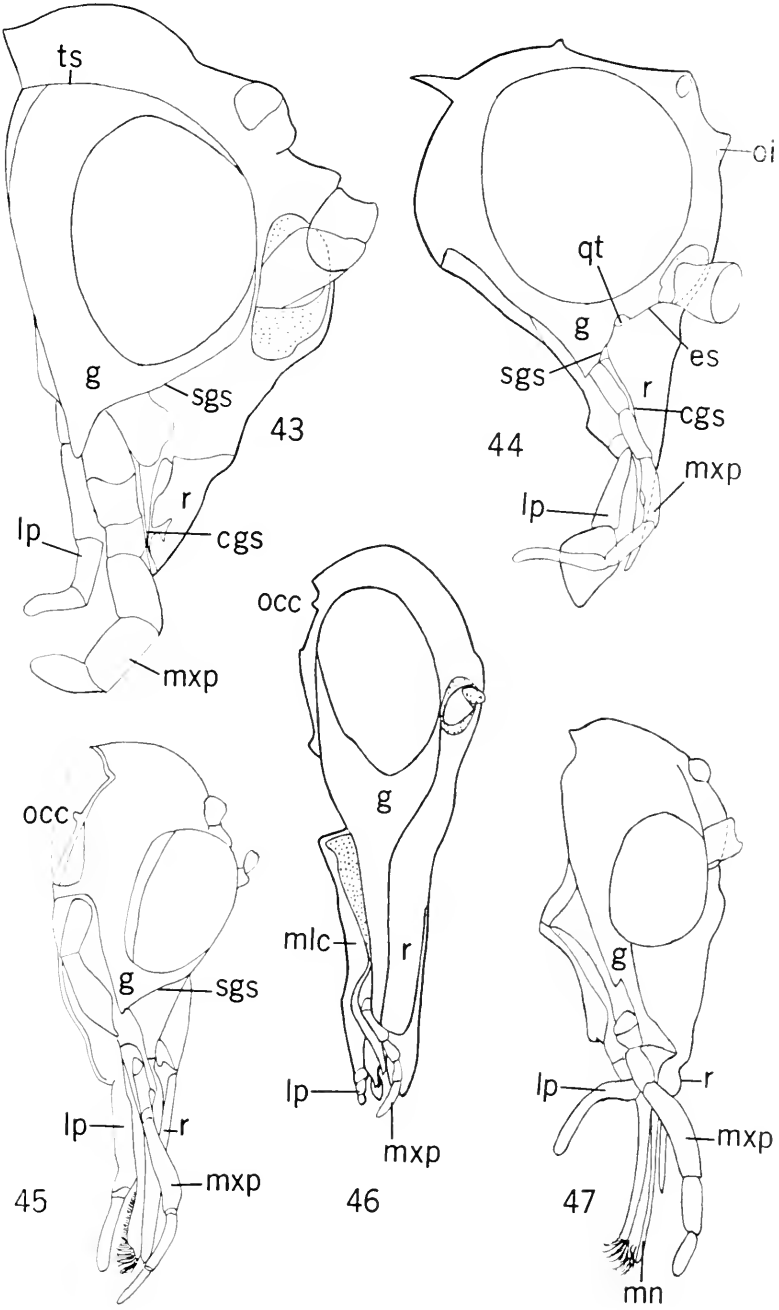

FIG. 43. *Brachypanorpa carolinensis*. Lateral view. FIG. 44. *Nannochorista dipteroides*. Same. FIG. 45. *Bittacus chlorostigma*. Same. FIG. 46. *Boreus unicolor*. Same. FIG. 47. *Apterobittacus apterus*. Same.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVIII   Pages 767-783   November 14, 1969   No. 18

The Morphology and Anatomy of *Alethopteris lesquereuxi* Wagner[1]

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ABSTRACT

The morphology and anatomy of numerous specimens of *Alethopteris* leaves found in Middle Pennsylvanian Kansas coal balls are described from observations based on fractured surfaces showing entire pinnae with pinnules, and serial peel thin sections showing details of internal anatomy. The specimens are identified as being equivalent to the compression species, *A. lesquereuxi* Wagner. Observations are made on the comparative anatomy of leaves of *Alethopteris sullivanti* and *A. lesquereuxi* and the extant *Cycas revoluta.*

INTRODUCTION

The form genus *Alethopteris* was established by Sternberg (1825) for certain Upper Paleozoic fern-like leaf compressions which have since proven to be an abundant and widespread element of the world's Pennsylvanian flora. A wide range of forms have been recognized, with the recent excellent monographic work of Wagner (1968) listing 29 species and 4 varieties.

The affinity of the leaves to the pteridosperms has long been recognized, both because of the constantly sterile pinnules (lacking any of the usual fern sporangia) and also because of the occasional discovery of specimens with large seeds attached (Halle, 1927). The frequent association of the *Alethopteris* leaf compressions with compressions of the medullosan pollen bearing organ, *Dolerotheca,* and seeds, *Pachytesta,* also suggest, even more specifically, that *Alethopteris* constituted at least one of the leaf types borne by the stem organ genus *Medullosa.* This suggestion is strengthened by the anatomical evidence found in coal balls, where it has been shown (Leisman,

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[1] This is part of a general investigation of the Pennsylvanian Coal ball flora supported by the senior author's National Science Foundation grant GB 4933.

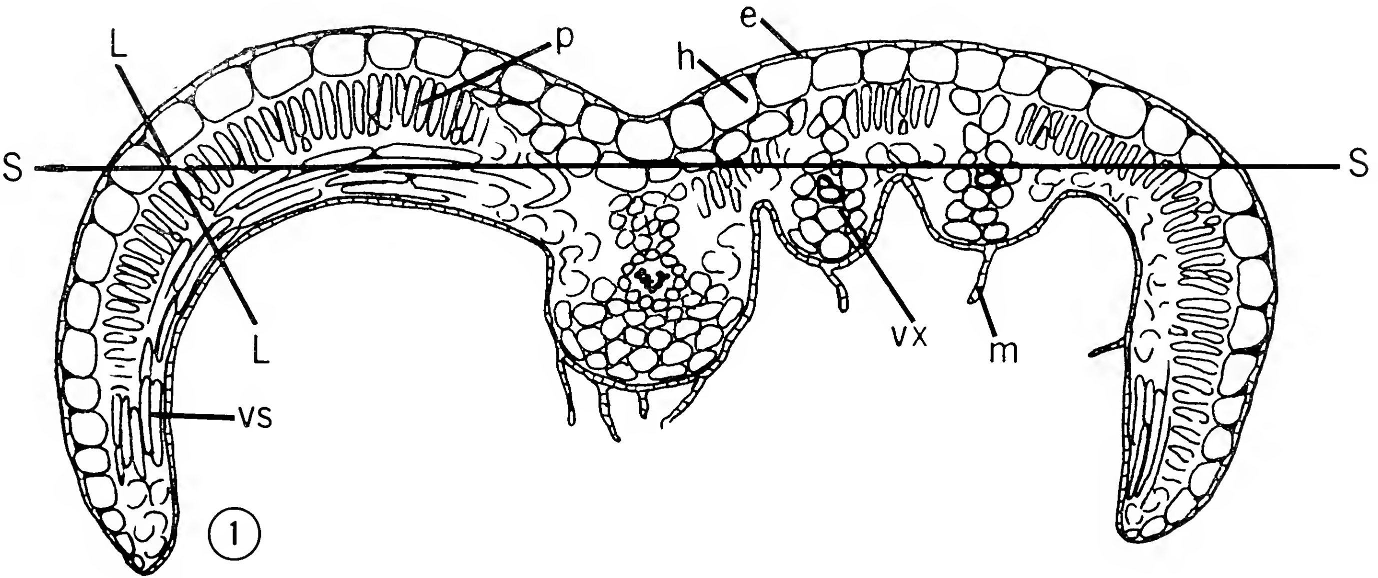

FIG. 1. *Alethopteris lesquereuxi.* Diagrammatic *cross section* of a pinnule showing planes of sections illustrated and discussed in text. Line (S) is a *sagittal section*, parallel to the broad surface of the pinnule. Line (L) is a *longitudinal section* at right angles to broad surface of pinnule. Left half of pinnule is sectioned parallel to lateral veinlets while right half of pinnule is sectioned at right angle to veinlets. *E*, epidermis; *H*, hypodermis; *P*, palisade layer; *VS*, veinlet side view; *VX*, veinlet transverse view; *M*, multicellular hairs. × 29.

1960) that similar mucilage canals, sclerotic strands and multicellular hairs, as well as numerous scattered collateral vascular bundles, are found in both the medullosan petiole *Myeloxylon* and the rachis and mid-ribs of *Alethopteris sullivanti* pinnules.

A comprehensive review of the synonymy and classification of the genus *Alethopteris* is given by Wagner (1968) and need not be repeated here. However, the revised generic diagnosis, based on his exceptionally complete monographic study, is worth quoting as a background for the following descriptions.

Generic Diagnosis (Wagner, 1968): "Repeatedly pinnate fronds which may attain large dimensions. Rachides usually striate. Pinnules strongly asymmetric, fused at the base, decurrent at the basiscopic side and decurrent, straight or slightly constricted at the acroscopic side. Pinnule lamina generally rather thick (giving a vaulted aspect to the pinnules). Lobing may be rather abrupt or more gradual, but lobing parts of the frond never seem to predominate. Nervation characterised by a well-marked midvein and numerous, non-anastomosing laterals attaining the pinnule borders at about right angles or somewhat obliquely (depending on the species). The lateral veins fork at irregular intervals. Subsidiary veins occur at the basiscopic side of the pinnule and generally at the acroscopic side as well. They either spring immediately from the supporting rachis or, more likely, derive from reclining basal lateral veins. Female fructifications ('seeds') of the *Trigonocarpus* and *Pachytesta* types. Male fructifications (as far as known) are bell-shaped synangia of the *Whittleseya* and *Dolerotheca* types."

Except for the paper by Leisman (1960) referred to above, all of the species of *Alethopteris* are known solely from compressions and impressions, and the much to be desired correlation of the details of the internal anatomy with those of the external morphology are generally lacking.

The purpose of our present study is to present such a correlation for specimens we believe to be equivalent to *Alethopteris lesquereuxi* Wagner which show both external morphology characters and internal anatomy comparable to that presented by Leisman for *Alethopteris sullivanti*. While Leisman originally described his material as *Callipteridium sullivanti*, both Wagner (1968, p. 151) and Cridland, Morris and Baxter (1963, p. 72) have pointed out that the proper assignment should be to *Alethopteris*.

MATERIALS AND METHODS

The present study is based on numerous specimens of *Alethopteris* found in coal balls from the Fleming coal of southeast Kansas. This is in the Cabaniss Formation, Cherokee Group, Desmoinesian Stage of the Middle Pennsylvanian which we believed to be equivalent to the upper part of the Westphalean D.

FIG. 2. *Alethopteris lesquereuxi.* Fractured surface of coal ball showing portion of frond. Note lack of visible lateral venation and deeply revolute lateral margins and apex of pinnules. Cross sections of pinnules exposed in fracture are shown at *(t)* with very large hypodermal cells clearly visible as white layer. × 6.

The specimens are contained in several dozen coal balls selected from some of the thousands which have been collected and cut in our laboratories over the past twenty years. From these, five different specimens of pinnae with pinnules showing the surface features (usually only seen in compressions) were obtained by splitting some of the coal balls along their natural fracture lines (Figs. 2-4). Numerous peel thin sections were also made in the three planes shown in Figure 1, the sagittal sections particularly being informative of details of venation which could not be observed in surface views.

GENERAL MORPHOLOGY

The pinnules average 3-4 mm wide by 8-10 mm in length, or proportionally around 2-3 times as long as they are broad. Both the pinnule lateral margins and apices are strongly revolute. The midrib is deeply sunken on the upper side, while the lateral venation pattern is very faint to lacking as viewed from the upper surface. The pinnule shape varies from nearly parallel sided, pecopterid forms on lower portions of the pinnae (Fig. 2) to pinnules with strongly decurrent lower sides (Figs. 3, 7) near the more apical portions of the pinnae. The bases of the pinnules are frequently swollen, forming a characteristic double bulge where they attach to the rachis (Fig. 4). The lateral veins, which generally can be seen only in internal, sagittal sections (Figs. 7-8), depart from the midrib at a slightly oblique angle at an average density of 32 per cm. The terminal pinnule is elongated and somewhat lanceolate.

INTERNAL ANATOMY

Transverse sections of the pinnules (Figs. 1, 6) present a somewhat M-shaped pattern due to the strongly revolute margins and the sunken, abaxially ridged midrib. The pinnules measure 720-750 μ in thickness near the middle of the lateral mesophyll, tapering gradually to a margin of scarcely 150 μ. This is much less than the equivalent measurements for *Alethopteris sullivanti*, where Leisman (1960) gives a 1445 μ thickness through the midvein and 635 μ in the middle mesophyll with little tapering at the non-revolute margins.

The upper epidermis consists of small, rectangular cells, which we have been able to see satisfactorily only in side views of cross and longitudinal sections of the pinnules (Figs. 1, 10, 13). In this view the cells measure 50 μ along their periclinal surface and only 20 μ in their anticlinal thickness. This layer is most frequently very poorly preserved and, along with the small size of the cells, quite difficult to see (Figs. 6, 11). Below this true but inconspicuous epidermis is a hypodermal layer of exceptionally large cells measuring 140 x 100 x 70 μ. In surface view their outer periclinal wall has

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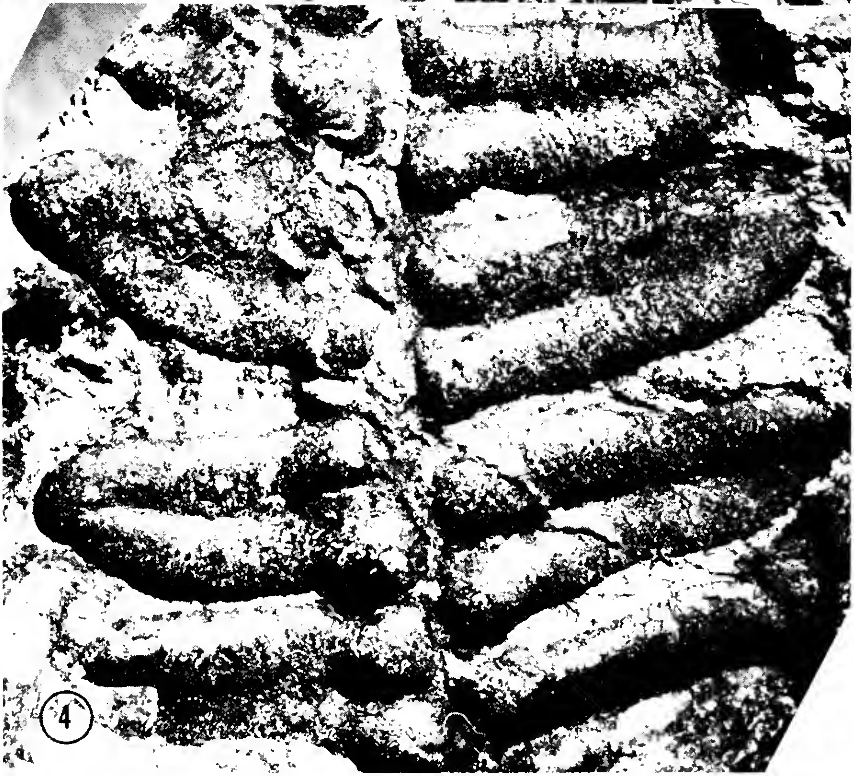

an irregular, pentagonal shape with the greatest width, which is parallel to the lateral veins, reaching 140 μ. In this view, where the upper epidermis has either naturally sloughed off or been removed by etching, they may simulate a fine reticulate venation reminiscent of the genus *Lonchopteris* (Fig. 5). Longitudinal sections of the pinnules, at right angle to the lateral veins, show the hypodermal cells are large rectangles measuring 70 μ across the top (periclinal) wall and 100 μ down the side (anticlinal) wall (Figs. 10-11). In cross sections of the pinnules, parallel to the lateral veins, the hypodermal cells measure 140 μ across the top (periclinal) wall and 100 μ down the side (anticlinal) wall (Figs. 1, 13).

This hypodermis seems identical to what Leisman (1960) called the inner layer of a double epidermis in *Alethopteris sullivanti*. However, since the determination of a double epidermis is dependent on knowledge of its ontogeny, it is obviously impossible to use the term here with certainty. Also, while a true double epidermis is known to occur in only a very few living plants, such as in the leaves of *Ficus* and *Peperomia* and roots of the orchids (Esau, 1965), hypodermal layers are quite common in many leaves, particularly in those of somewhat xerophytic character. Accordingly, the term hypodermis would seem most appropriate for this most distinctive tissue apparently common to both *A. sullivanti* and *A. lesquereuxi*. Indeed, while the relative development of the cuticle, palisade and spongy tissues of an extant species may vary with ecological changes, the presence or absence of a hypodermis will normally be a constant taxonomic character. Accordingly, the proof that two such dissimilar species of *Alethopteris* have this concurrence of a minute upper epidermis subtended by a large hypodermis suggests that it may be a character common to the genus. It is not, to our knowledge, a feature found in any other coal ball leaves.

Immediately below the hypodermal layer is the palisade tissue, consisting of one to two layers of vertically elongated cells which are characterized in nearly all of our material by their opaque, black contents (Fig. 11). This tissue constitutes approximately one half of the mesophyll thickness below the hypodermis, the balance consisting of a loosely arranged spongy tissue with numerous air spaces (Figs. 9, 11).

The midrib vascular bundle enters directly from the lower side of the flattened rachis (Figs. 7-8). It consists of 16-20 primary tracheids, the small-

FIGS. 3-4. *Alethopteris lesquereuxi*.

FIG. 3. Fractured surface of coal ball showing apical portion of a frond. Original cut of coal ball resulted in loss of tip of apical pinnule, but visible portion indicates the elongate-lanceolate shape characteristic of the species. A fracture through mesophyll of pinnule shows a sagittal section at *S*. × 6.

FIG. 4. Fractured surface of coal ball of still another specimen. Note deeply sunken midrib, revolute margins, double swellings at pinnule bases, and absence of visible lateral veins. × 6.

FIGS. 5-6. *Alethopteris lesquereuxi.*

est of which are on the abaxial side, making the structure apparently exarch. The xylem is directly enclosed in a bundle sheath 200 μ in diameter with collenchyma type sheath extension cells extending to the upper hypodermis and lower epidermis. No phloem can be recognized.

The lateral veins depart from the midrib at a slightly oblique angle towards the pinnule apex and usually dichotomize once before reaching the margin (Figs. 7-9). They pass through the spongy tissue slightly below the palisade layer (Fig. 11) and are constantly of such small size that the term "veinlet" seems appropriate for them. The xylem of each veinlet consists of only 3-5 primary tracheids, ranging in diameter from 10 to 20 μ, showing an apparent exarch development (Fig. 10).

The conspicuous bundle sheath tightly encloses the xylem strand, and no tissue recognizable as phloem could be identified. The bundle sheath consists of parenchymatous tubular cells, 40 x 500 μ long, elongated parallel to the veinlet (Figs. 9-11). Similar bundle sheath extension cells extend upwards to or through the palisade layer but never beyond the hypodermis. On the lower (abaxial) side, the sheath extensions widen out and become more sclerotic, forming the buttresses for the conspicuous ridges which characterize the lower surface of the pinnules (Figs. 10-11). The entire diameter of the veinlets, including the bundle sheath, is 120-140 μ, with their density (measured near the pinnule margin) averaging 32 per cm.

Subsidiary veins can be seen entering the base of the pinnules *directly from the upper side of the flattened rachis* (Fig. 7). Accordingly, in this species at least, there can be no doubt that separate subsidiary veins do exist in *Alethopteris* and that the situation is not as described by Bocheński (1960) but rather as diagramed by Wagner (1968, p. 25, text fig. 1). Consequently, Wagner's generic diagnosis, quoted earlier, should probably be revised to emphasize this direct rachis origin of the subsidiary veins.

There is certainly no evidence, in all of the many sagittal sections of *A. lesquereuxi* examined, to support the concept of a single, strong, decurrent midvein. Quite to the contrary, as many as 5-6 subsidiary veins appear to enter the bases of decurrent pinnules directly from the upper side of the flattened rachis, with the independent midrib vein entering the pinnule from a lower level of the flattened rachis. This feature of independent vascular strands is undoubtedly related to the numerous separate vascular

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FIG. 5. Pair of pinnules exposed on fractured surface of coal ball. Note reticulate pattern of large hypodermal cells exposed here by etching away the upper epidermis. Fracture of tip of lower pinnule has exposed a cross section showing the large hypodermal cells in side view and deeply incurved revolute pinnule margins. *h*, hypodermis in face and side views. × 10.

FIG. 6. A peel cross section of a pinnule. Adaxial midrib furrow lacking due to section being near pinnule apex (see pinnules upperleft part of Fig. 2). Compare to Fig. 1, which represents cross section near middle of pinnule. *e*, epidermis; *h*, hypodermis; *t*, multicellular epidermal hairs. × 60.

Figs. 7-8. *Alethopteris lesquereuxi.* Peel thin sections in sagittal plane through pinnules showing pattern of lateral veinlets.

bundles already known to occur in the *Alethopteris* rachis (Leisman, 1960), which is apparently an extension of the multi-bundled anatomy of the *Medullosa* petioles.

The lower epidermis appears to be a continuation around the pinnule margins of the same uniseriate layer of very small cells found on the upper side. As on the adaxial side, they are poorly preserved and usually only evident as a thin amorphous black layer subtending the veinlet ridges and the alternate furrows. Efforts to obtain free epidermal tissues by maceration were not successful, nor could stomata be pinpointed with any assurance. It would seem very likely, however, that stomata were present on the lower surface in the furrows between the veinlet ridges. There seems no reason to doubt, considering other basic similarities between *A. sullivanti* and *A. lesquereuxi*, that the stomata are probably also of the haplocheilic type.

Numerous uniseriate, multicellular hairs arise from the lower epidermis. They are particularly abundant on the midrib and veinlet ridges and also near the inner side of the revolute pinnule margins (Figs. 1, 6). Pappilate cells such as described for *A. sullivanti* (Leisman, 1960) appear to be lacking.

DISCUSSION

The assignment of our coal ball specimens to *A. lesquereuxi* Wagner is based on strong similarities in the size, shape and revolute margins of the pinnules. The angle and number of lateral veinlets per cm also agrees with Wagner's specific diagnosis as does the form of the terminal pinnule. Photographs of the specimens exposed on the fractured surfaces of the coal balls (Figs. 2-4) were also sent to Dr. Wagner, who independently arrived at an identification with *A. lesquereuxi*.

Since *Alethopteris sullivanti* and *A. lesquereuxi* now constitute the only two species in which both external morphological and internal anatomical characters are fully known and correlated, it may be worthwhile to summarize the anatomical features in which they agree versus the ones in which they differ. In this way we may be able to emphasize what seem to be generic versus specific characters. On this basis, the characters common to the genus appear to be: (1) the presence of a thin, small celled upper epidermis subtended by a hypodermis of conspicuously larger cells; (2) dif-

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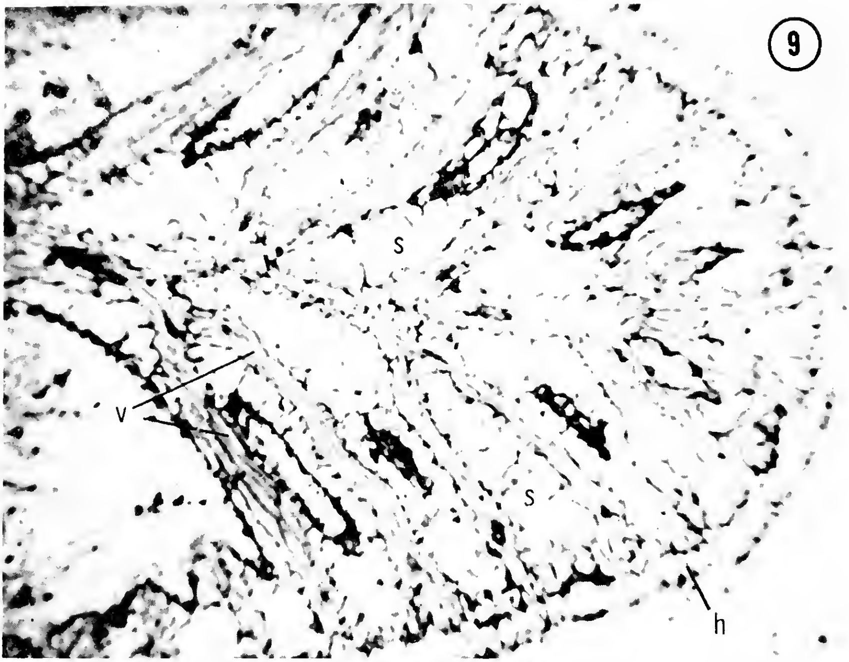
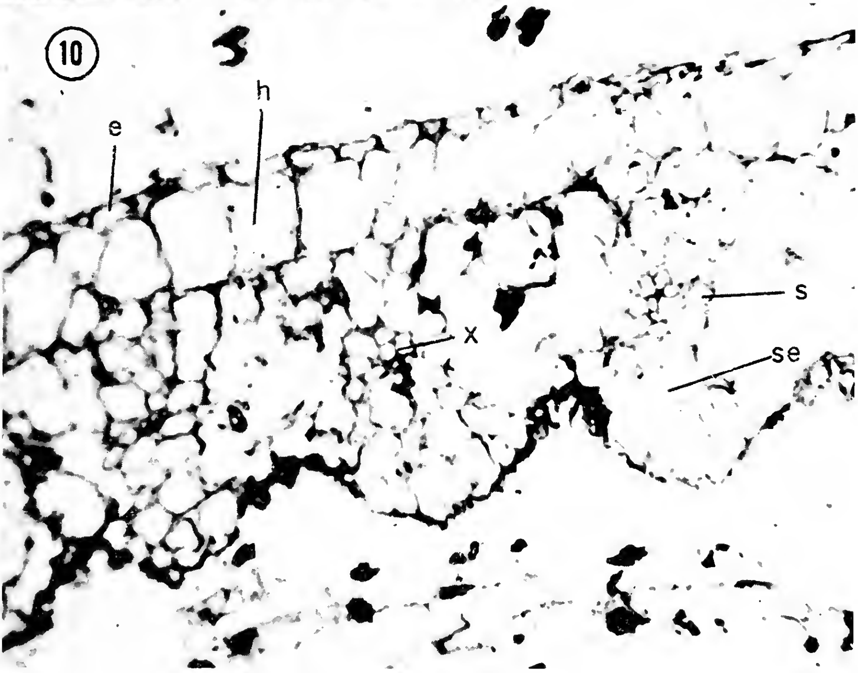
FIG. 7. A portion of the rachis (*R*) with two attached decurrent pinnules. Section passes above sunken midrib, the position of which is shown at *M*. Susidiary veins (*V*) can be seen entering base of pinnule directly from rachis. × 10.

FIG. 8. Nearly complete pinnule at upper left shows midrib and lateral veins near apex, while section in basal part has been cut above sunken midrib through large cells of hypodermal layer. The bases of the two pinnules on the right margin appear as double-compartmented boxes due to the sagittal section passing below the main pinnule and showing only the sunken midrib and the revolute margins. *h*, hypodermis; *T*, tissue of sunken midvein; *R*, revolute pinnule margin. × 10.





FIGS. 9-10. *Alethopteris lesquereuxi.*

ferentiation of the mesophyll into an upper palisade layer and a lower spongy layer; (3) parenchymatous bundle sheathes and bundle sheath extensions; (4) numerous bundles in rachis; (5) uniseriate multicellular hairs on lower epidermis.

The anatomical characters in which the species differ are as follows: (1) Size of epidermal and hypodermal cells. In *A. sullivanti* the epidermis consists of cells 19 x 31 μ with the cells of the hypodermis averaging 43 x 43 μ. In *A. lesquereuxi* the comparable measurements are 20 x 50 μ for the epidermis and 100 x 70 μ for the hypodermis as seen in longitudinal section of the pinnules (our Fig. 10 and Leisman, 1960, fig. 7); (2) the pinnules are thicker in *A. sullivanti*, measuring 635 μ in the blade to 540 μ for *A. lesquereuxi*, with a corresponding variation in thickness of the palisade and spongy layers of the mesophyll; (3) the lower surface of the pinnule of *A. lesquereuxi* is ridged below the veins while the lower surface is smooth in *A. sullivanti*; (4) *A. sullivanti* pinnules are flat with little tapering at the margins contrasted to *A. lesquereuxi* pinnules which have strongly revolute, tapered margins.

The primary xylem of the veins in *A. sullivanti* is described as endarch while that of the veinlets and midvein in *A. lesquereuxi* seems to be exarch. It is doubtful that this is a real difference since observations regarding the relative position of protoxylem and metaxylem, which are inferred solely from tracheid size as seen in cross sections, are dubious to say the least. The size range of the tracheids and the shape of the xylem strand in our specimens (Figs. 10, 12) seems suggestive of exarch development but certainly cannot be held to be conclusive.

While the leaves of both species seem to show some xerophytic characters, e.g. hypodermis, thick mesophyll, and abundant multicellular epidermal hairs, the trend appears more strongly developed in *A. lesquereuxi*. This inference is based on the much thicker hypodermal layer, the probable restriction of stomata to furrows sunken between the veinlet ridges and the deeply revolute margins which may have also functioned to reduce air flow over the stomatal area. The hypodermal layer of *A. lesquereuxi* is particularly striking since, while uniseriate, it still may contribute as much to the pinnule thickness as the entire palisade tissue.

Wagner's (1968) monograph of *Alethopteris* indicates a wide distribution for *A. lesquereuxi* in strata of late Westphalean D to strata of lower

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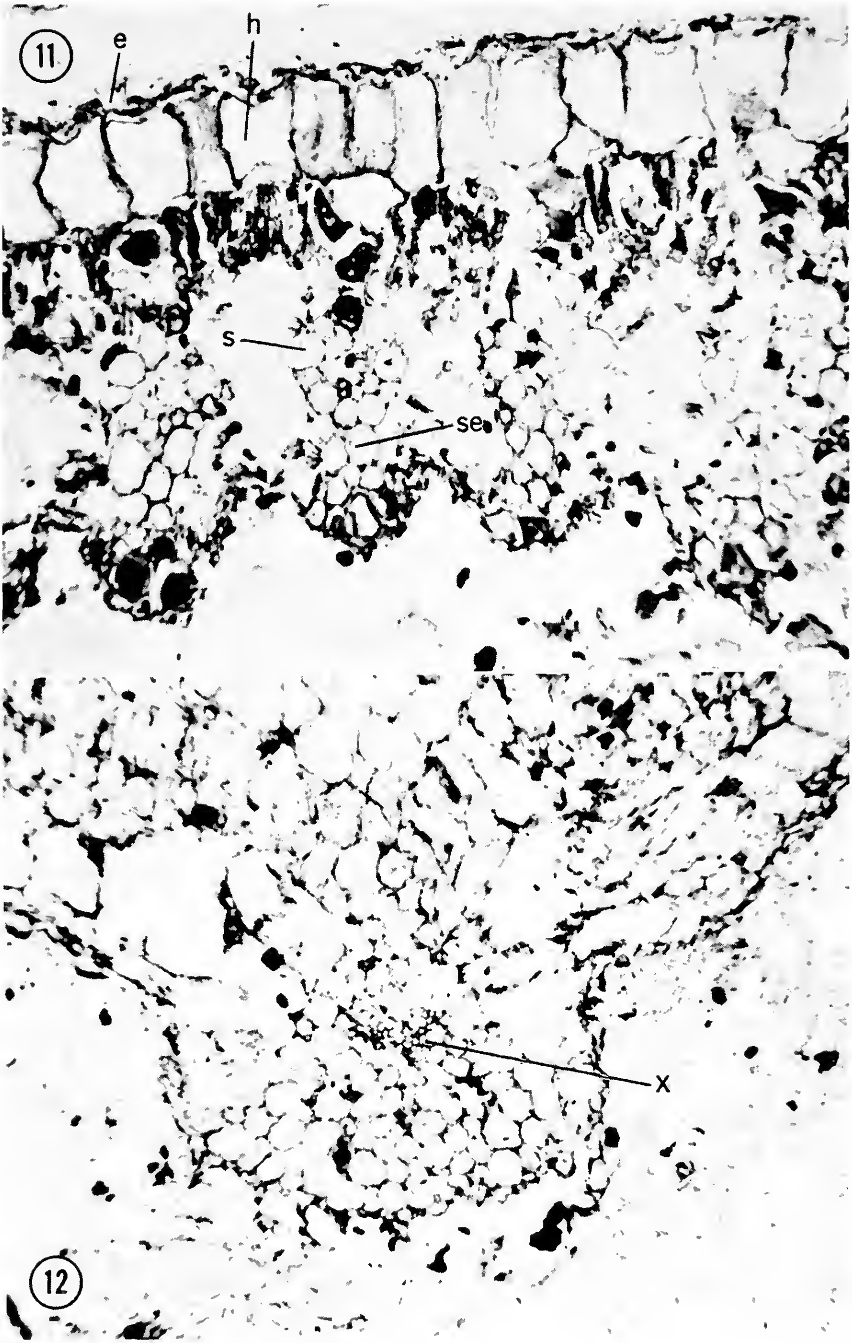
FIG. 9. Peel section through sagittal plane of pinnule tip showing dichotomous lateral veinlets *(V)* passing through spongy tissue *(S)*. Elongate cells shown are those of the veinlets' bundle sheaths. *h*, hypodermal layer exposed at revolute margin. × 33.

FIG. 10. Longitudinal section of pinnule near margin. *e*, epidermis; *h*, hypodermis; *x*, xylem; *s*, bundle sheath; *se*, bundle sheath extension. Palisade and spongy tissues are diminished due to section being very close to pinnule margin. Note abaxial ridges below veinlets. × 120.



Figs. 11-12. *Alethopteris lesquereuxi.*

and middle Stephanian age in Spain, Great Britain and North America. It is certainly the dominant species in the Middle Pennsylvanian coal ball flora of Kansas since, other than the occasional *A. sullivanti* specimen, almost all of the identifiable material in our collections now seems assignable to *A. lesquereuxi*.

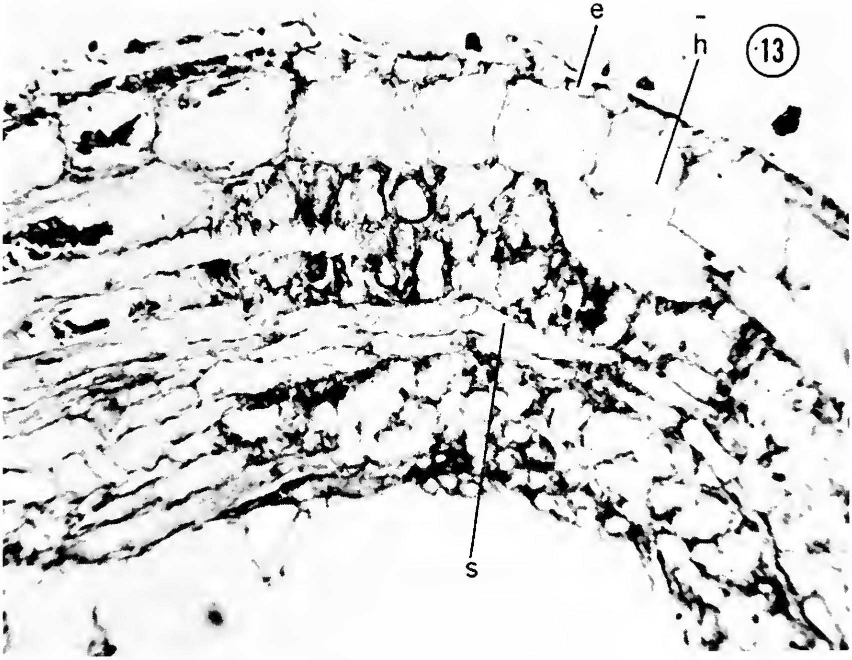
Since a possible relationship between the genus *Medullosa* (which almost certainly bore these leaves) and the living cycads has frequently been postulated on various features of stem anatomy, seed position, etc., a comparison of the leaf structure in *A. lesquereuxi* and the extant *Cycas revoluta* is shown in Figures 13 and 14. It may be noted that both have a thin epidermis subtended by a much larger hypodermis. Also, while *Cycas revoluta* is described (Coulter and Chamberlain, 1917) as lacking lateral veins, it does show the presence of long tubular parenchyma cells with large conspicuous pits which extend outwards from the midrib to the pinnule margins and possibly function as a kind of transfusion tissue. As can be seen in Figures 13 and 14, these cells are strikingly similar to the bundle sheath cells in *A. lesquereuxi* which, because of the minute amount of vascular tissue, probably were also functional in water conduction. A reduction theory might be developed leading from the rather large veins of *Alethopteris sullivanti* to the small veinlets of *A. lesquereuxi* to *Cycas revoluta* where the vascular portion of the lateral veinlets has been completely lost.

Certainly the lateral veinlets in *Alethopteris lesquereuxi* are so small and separated from the upper blade surface by the large hypodermis, that it is doubtful that the living, uncompressed pinnules would have shown any pattern of lateral venation on the upper surface (Figs. 2, 5), but instead would seem to have only the single midvein as in *Cycas revoluta*.

The extremely primitive megasporophyll of *Cycas revoluta* makes it a particularly attractive subject for comparison to the seed ferns, but one could as equally well postulate an evolvement of the leaves of the other genera of extant cycads from the seeming vascular reduction in *Alethopteris sullivanti* and *A. lesquereuxi*. For example, the numerous basal dichotomies leading to the apparent parallel venation of *Zamia, Dioon, etc.* could be derived from the individual "subsidiary veins" of *Alethopteris* with a reduction in size of the midvein, while *Stangeria*, with its midrib and dichotomous lateral veins, could represent a form with relatively unmodified venation.

FIG. 11. Peel longitudinal section through thicker portion of pinnule than shown in preceding figure. *e*, epidermis; *h*, hypodermis; *s*, bundle sheath; *se*, bundle sheath extension. Some palisade tissue visible below hypodermis. Note abaxial ridges below veinlets. × 120.

FIG. 12. Transverse section of pinnule mid-rib. *x*, primary xylem of bundle, apparently exarch. × 50.



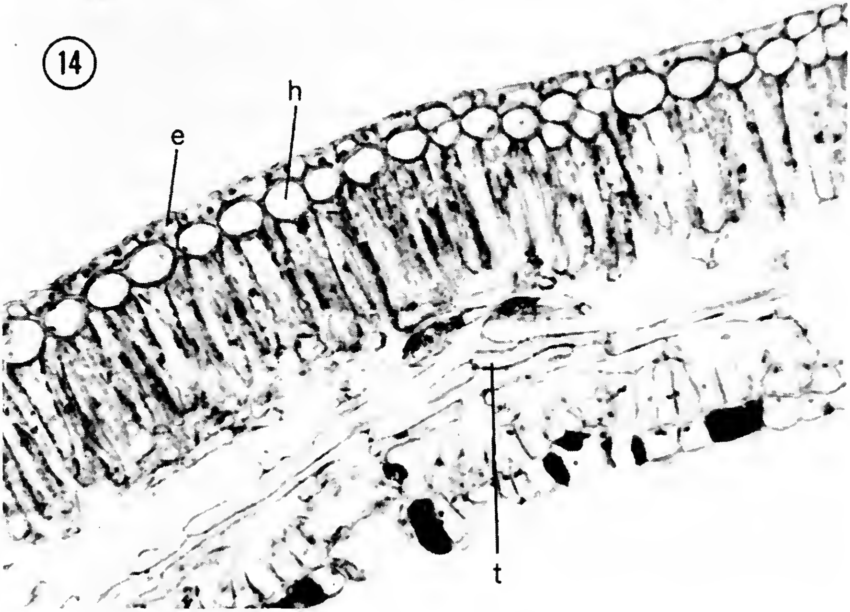


FIG. 13. *Alethopteris lesquereuxi.* Cross section of a portion of a pinnule cut parallel to a lateral veinlet. *e,* epidermis; *h,* hypodermis; *s,* elongated cells of bundle sheath. × 120.

FIG. 14. *Cycas revoluta.* Cross section of a portion of a pinnule showing elongate "transfusion" cells *(t).* *e,* epidermis; *h,* hypodermis. × 135.

If one continues in this purely theoretical argument, it can be postulated that the obvious xerophytic modifications in the extant cycads led to a reduction in frond size from the very large multi-pinnate leaves of *Medullosa* to the once pinnate (bipinnate in *Bowenia*) leaves of the present cycads, along with a reduction in lateral venation as a mechanism to diminish water loss.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVIII Pages 785-790 November 14, 1969 No. 19

On the Status of *Caecilia occidentalis* Taylor

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While re-examining caecilians in the Academy of Natural Sciences of Philadelphia (ANSP), I found four specimens from Popayan and Moscopán, Cauca, Colombia, which had been overlooked on my previous examination of the collection. These had been labeled *Caecilia pachynema* by a previous caretaker. Careful examination of these specimens causes me to associate them with *Caecilia occidentalis* Taylor described from a specimen obtained from Dr. Max Hensley and likewise from Popayan. Despite the fact that the specimen serving as the type had been injured badly, practically all significant characters were discerned.

Of these four specimens, ANSP Nos. 25566-25569, the first three are topotypes of *C. occidentalis*, the fourth is from Moscopán, Cauca, Colombia. They provide data to substantiate the validity of the species. A skull has been prepared from ANSP No. 25568, which is described and figured.

Comparative data on measurements, tooth counts, etc., are presented in the following table [data on the type, (EHT-HMS 4665), included].

From the table, it will be noted that the process of growth entails a great lengthening of the body, the width of head and body growing but little proportionally.

The absence of secondaries in certain specimens of a species has been reported in other species of the genus *Caecilia* (i.e., *guntheri*, *pachynema*) while in certain other species secondaries have not as yet been found to occur (i.e., *caribea* and *elongata*).

The collars in these four specimens are not as well marked as in the type. The transverse dorsal grooves are either absent or only dimly indicated. The two collars are not clearly separated dorsally, and the second is fused dorsally and ventrally with the first primary fold.

The lateral cream or yellowish stripe is similar to that of the type, better defined anteriorly and posteriorly, while in the area between, it may be reduced to a dim broken line which may be absent for a distance. The

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TABLE 1. Comparative data on *Caecilia occidentalis.* All measurements are in mm.

Museum No. Locality	EHT-HMS 4665 Popayan	ANSP 25566 Popayan	ANSP 25567 Popayan	ANSP 25568 Popayan	ANSP 25569 Moscopan
Total length	1035	425	564	868	995
Head width	10	7	8	8	9
Body width	9.3	8.2	8.5	8	9
Eye to tentacle	5.4	3.2	3.5	4	4.1
Tentacle to nostril	1.7	1.1	1.25	1.5	1.6
Primary folds	218	191	209	205	221
Complete folds	4 or 5	5	8	17	20
Secondary folds	0	12	0	4	8
Premax-max. teeth	12-13	8-8	10-9	11-11	11-10
Prevom-pal. teeth	10-11	10-9	11-12	12-12	12-11
Dentary teeth	11-11	12-(12)	12-12	12-12	11-11
Splenial teeth	5-(5)	3-3	3-3	3-3	3-3
Scales (rows) posteriorly	1	1	1	1	1
Width in length (times)	111	52	663	1085	110
Vertebrae	225	197	207	212	229

subterminal markings are practically the same in all. The occipital region may have three dim cream spots and there is a more or less distinct light spot at or anterior to the tentacle and the nostril; one also on the tip of the snout.

Scales in the grooves are present in more than two thirds of the body. Subdermal scales, in evidence throughout much of the body, are very small, rarely more than 0.2 mm in diameter. The head is generally tapering somewhat, the snout extending about 2.0 to 2.3 mm beyond the mouth. Within the mouth the choanae are very close to the prevomerine teeth. The narial plugs of the tongue are elevated and teatlike.

The skull of this species shows strong similarity to the skulls of the Caeciliinae, especially to species of the *Caecilia sensu strictu,* as the data here recorded indicate. The data presented are from the skull of ANSP 22568. The skull agrees with skulls of the family in having the reduced number of bones. Thus the prefrontals, septomaxillae and oculars are not present as separate bones. The nasals and the premaxillary elements are fused to form the nasopremaxillae. The maxillae and palatines are fused to form the maxillopalatines. The stapes are present. The mesethmoid does not appear on the dorsal surface of the skull.

The anterior dorsal surface of the skull is covered by the paired nasopremaxillae, the lateral edges of which are roughly notched along the

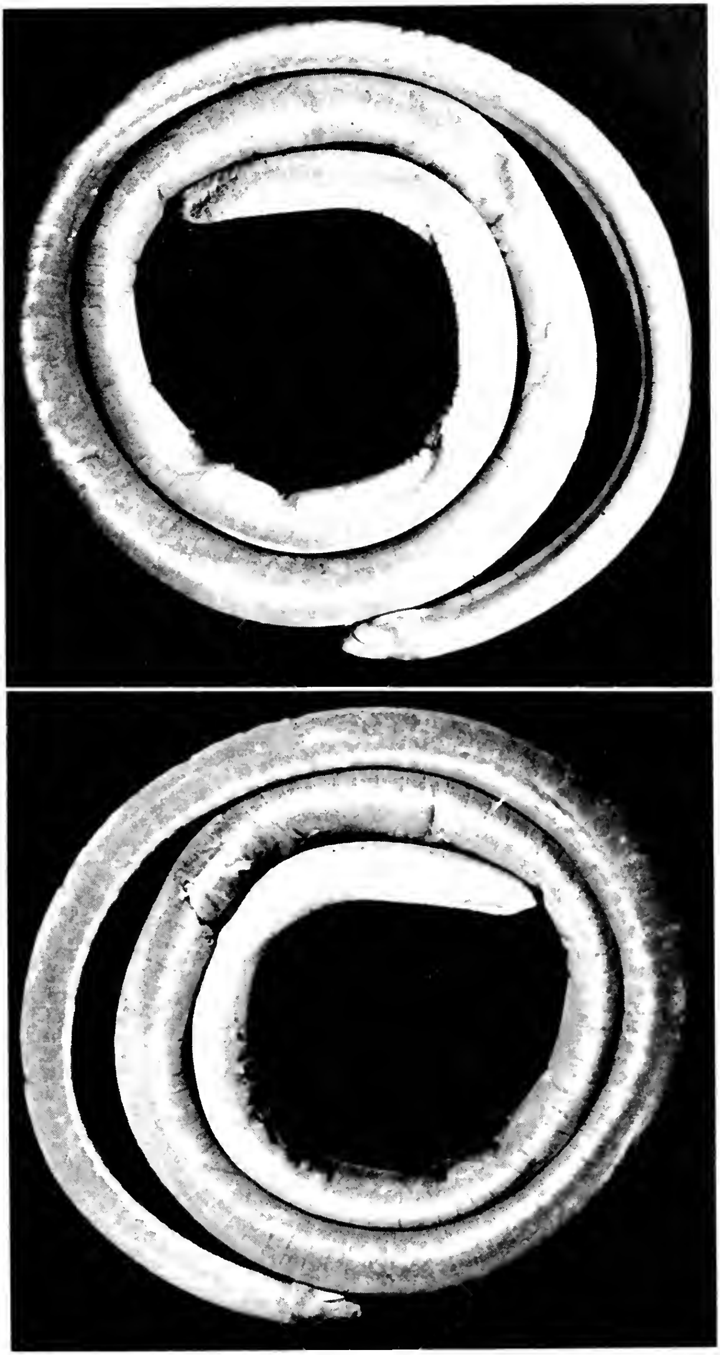

Fig. 1. Left. Left lateral view of *Caecilia occidentalis* Taylor. Topotype. ANSP No. 25567, Popayan, Cauca, Colombia. Total length, 564 mm. Right. Right ventrolateral view of the same specimen.

sutures. The frontals are narrowed anteriorly, flaring out posteriorly, in contact only for about one half of their length. The parietals are a little longer than the frontals, bending down posteriorly with very uneven sutures. The two lateral posterior parts of the compound basisphenoid meet narrowly preceding the foramen magnum.

The side of the skull anteriorly is formed by the maxillary part of the maxillopalatine, followed by the squamosal, a bone somewhat shorter than the preceding, and in contact posteriorly with the quadrate and also to a process of the stapes.

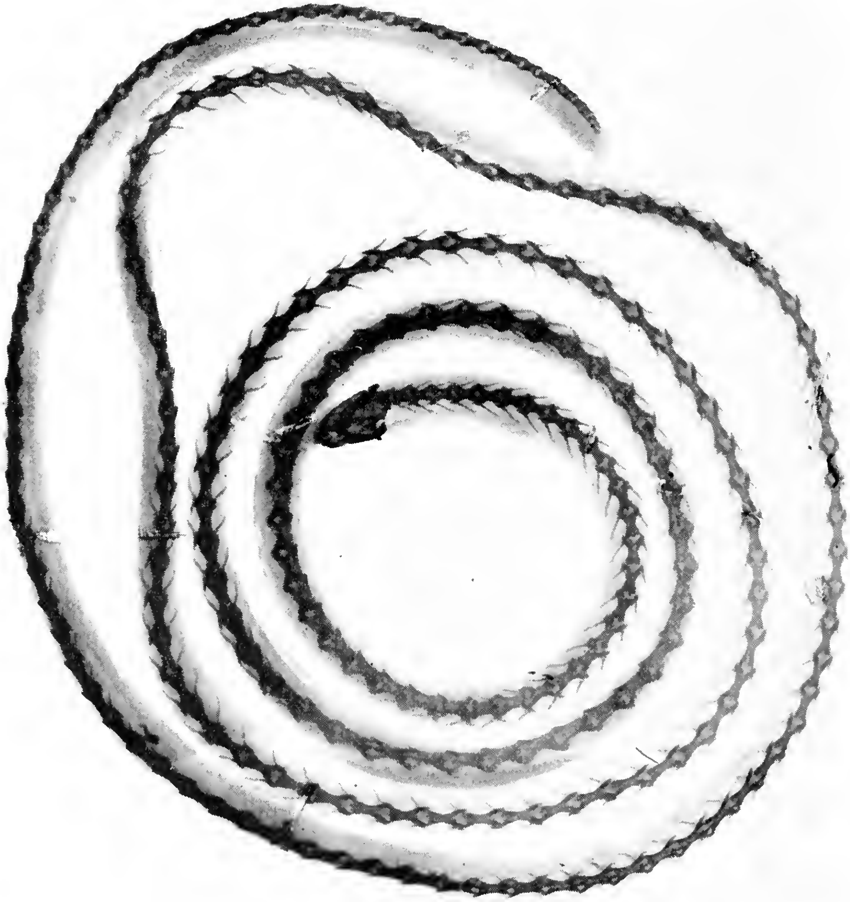

FIG. 2. X-ray of *Caecilia occidentalis* Taylor. ANSP No. 22569, Moscopan, Cauca, Colombia. Vertebrae, 229. Actual length, 995 mm.

The stapes fits into a notch in the lateral part of the basisphenoid. The posterior part of the suture between the parietal and squamosal is joined by cartilage.

Anteriorly on the ventral surface of the skull there is a shelflike forward projection between the nasal openings. The premaxillary parts of the nasopremaxillae bear seven teeth (3-4). On the ventral side of these parts there are three posterior projections which interdigitate with two blunt processes from the anterior part of the prevomers preceding the prevomerine dental series. These series consist of seven teeth (3-4). The prevomerine bones extend posterior to the teeth, separated for much of their length by an anterior spine of the basisphenoid and reaching one fourth of their length behind the internal nares, forming half of the border of the nares on their inner sides. The outer sides of the nares are bordered by the palatine portion of the maxillopalatine.

The basisphenoid sends forward a spinelike process that separates the prevomers for more than half their length, and also two processes between the prevomers and the relatively small diastema between the basisphenoid and the pterygoid process of the quadrate. The "wings" of the basisphenoid are large, laterally curving down slightly. Below the region of the otic capsules there are two short, transversely flattened, blunt, processes.

The skull measurements in mm and tooth counts are as follows: total length of skull, 11.2; greatest width, 6; width at orbits, 5; length of jaw, 7.2; length of basisphenoid (ventral), 8; width of same at "wings," 4; width at otic capsules, 4; length of prevomers, 5.2; width of prevomers, greatest, 3; length from anterior edge of internal nares to occipital condyle, 6.4; premaxillary teeth, 3-4; maxillary teeth, 7-7; prevomerine teeth, 4-4; palatine teeth, 8-7; dentary teeth, 13-13; splenial teeth, 4-4. Total length of the preserved specimen, 868.

I desire to extend my gratitude to The Director of the Philadelphia Academy of Sciences, Dr. Radclyffe Roberts, and to Dr. James E. Böhlke, Curator, for the loan and for assistance while at the Academy.

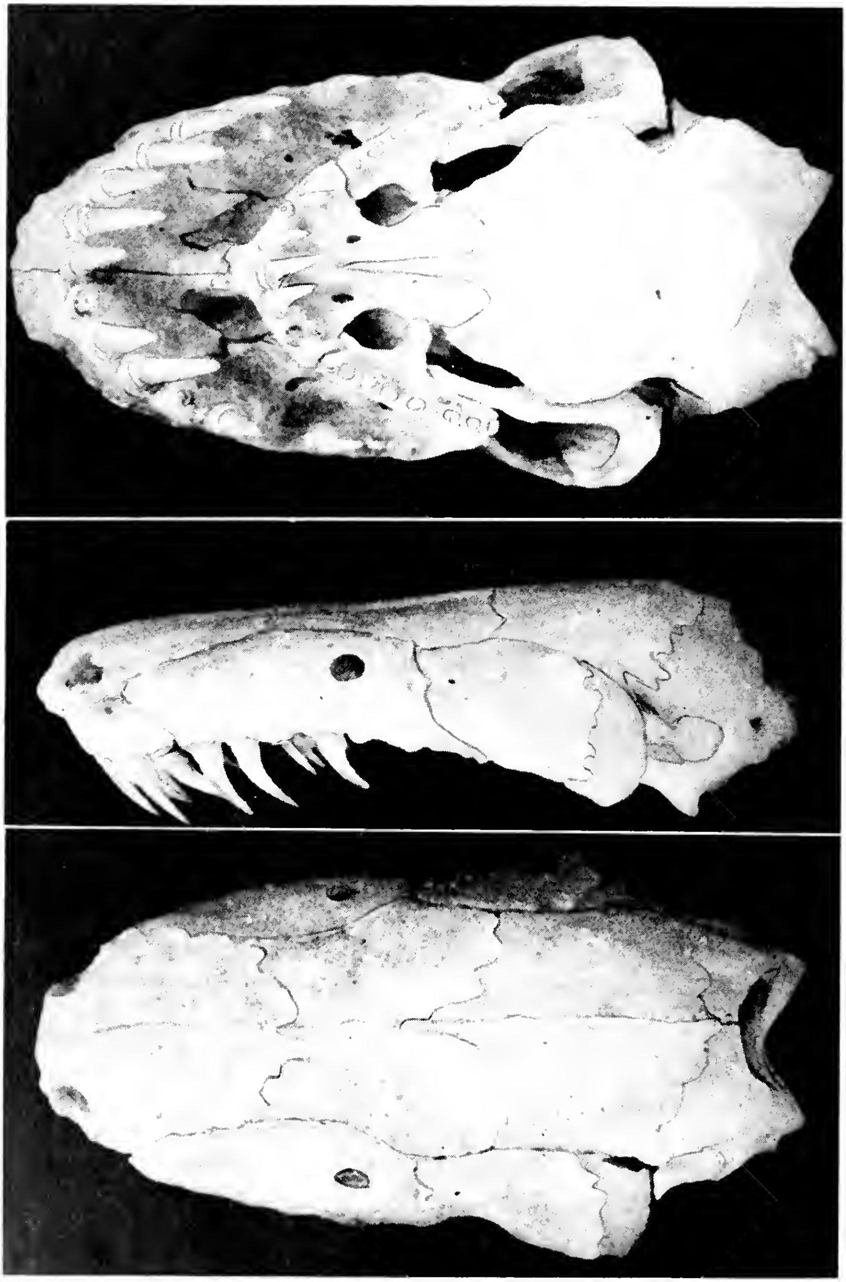

Fig. 3. Three views of the skull of *Caecilia occidentalis* Taylor: dorsal, lateral, and ventral. ANSP No. 25568. Length of skull, 11.2 mm; greatest width, 6.0 mm.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

VOL. XLVIII PAGES 791-799 JANUARY 9, 1970 No. 20

Dental Abnormalities in North American Bats. II. Possible Endogenous factors in Dental Caries in *Phyllostomus hastatus*

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Dental decay is a complex disease that has been studied intensively in man, strains of the Norway rat *(Rattus norvegicus)*, and in a few other laboratory mammals. Many different endogenous and exogenous factors have been analyzed (see Keyes and Jordan, 1963). It is thought, however, that the basic biochemical, physiochemical, and physical factors that interact to cause dental caries are comparable in all mammals (König, 1965). Although laboratory and clinical studies are numerous, there have been only a few reports of the incidence and causes of dental caries in wild mammals (Colyer, 1936; Hall, 1940, 1945), and no previous study of this disease in bats has been undertaken. In the course of studies of the dentitions of North American Chiroptera, we discovered a high incidence of dental caries in the spear-nosed bat, *Phyllostomus hastatus*, but no evidence of the disease in related species. When disease of any kind is found commonly in one species, but not in closely related kinds, the causes and evolutionary implications of that disease become important areas for investigation.

Among 52 specimens (all adults) of *Phyllostomus hastatus* examined from Nicaragua, Panama, Trinidad, and Venezuela, 21 (40.4%) of the individuals had readily detectable dental caries, resulting, in many cases, in the loss of one or more teeth. The incidence of carious lesions in males (75% of 20 specimens) was found to be significantly greater ($p \geqq .99$) than in females (18.7% of 32 specimens). Occurrence of the disease evidently is not geographically variable, because specimens from each of the regions listed had carious lesions. No evidence of dental caries was found, however, in 103 specimens of *Phyllostomus discolor* from Chiapas, Guatemala, Nicaragua, and Trinidad, nor in 12 specimens of *P. elongata* from Peru, nor were

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carious lesions found in individuals of other phyllostomatine genera studied (*Micronycteris, Macrotus, Chrotopterus, Mimon, Tonatia, Trachops, Lonchorhina,* and *Macrophyllum*). Furthermore, among 1500 specimens examined of species in the families Emballonuridae, Noctilionidae, and Chilonycteridae, but one bat was found with dental caries (Phillips and Jones, 1969).

Specimens of *Phyllostomus* were examined grossly for carious lesions, which, when discovered, were recorded as to site and severity. External morphological features of the teeth visible with a binocular dissecting scope were correlated with the occurrence of lesions. For comparative histological studies and further analysis of possible endogenous factors, teeth of several *P. hastatus* and *P. discolor* were demineralized in 5% nitric acid (48 hours), embedded in tissuemat and piccolyte at 56.5° C, sectioned at 9 μ, and stained with Mallory's triple. The material used for histological examination had been preserved in 10% formalin and stored in 70% alcohol. The teeth of *P. hastatus* and *P. discolor* were compared with regard to all visible surface characteristics as well as to histological features.

Dental caries in *P. hastatus* often begin in the third upper and lower molars and progress anteriorly. We base this statement on the fact that carious lesions were present and generally more advanced in these teeth in the 13 diseased individuals in which there were extensive caries in the molars (Fig. 1). Dental caries are of the acute type in *P. hastatus,* which results in the complete destruction of the crown and cervical region of diseased teeth. Following initial penetration of the enamel, the disease destroys the dentin leaving an enamel shell that is easily fractured and exfoliated (Fig. 1). Diseased teeth respond to infection in essentially the same ways as do human teeth: in some instances, there is extensive resorption of the cementum layer and dentin; in other instances, new layers of cement are added to the apical portion of the root of the traumatized tooth (Fig. 2).

The third molars of *P. hastatus* differ from the other cheekteeth in being the last to develop and attain the functional eruptive stage and in being the smallest. Furthermore, the labial surface (parastyle) of the upper third molar is covered by a thick ridge of tissue. This tissue covering varies individually but always is well developed in specimens having dental caries. The ridge of tissue begins on the labial surface of the mandibular epithelium and ends on the surface of the maxilla at the corner of the mouth. Consequently, a flap covers the labial coronal and cervical surfaces of the third upper molars. Debris accumulate (as can be seen in specimens preserved in alcohol) in the pocket between the surface of the tooth and the flap of tissue. Presumably, such an environment would provide an excellent substrate for bacterial infection. In *Phyllostomus discolor* the ridge and flap of tissue are either absent or are so reduced that the surface of the third molar is free and therefore subject to self-cleaning.

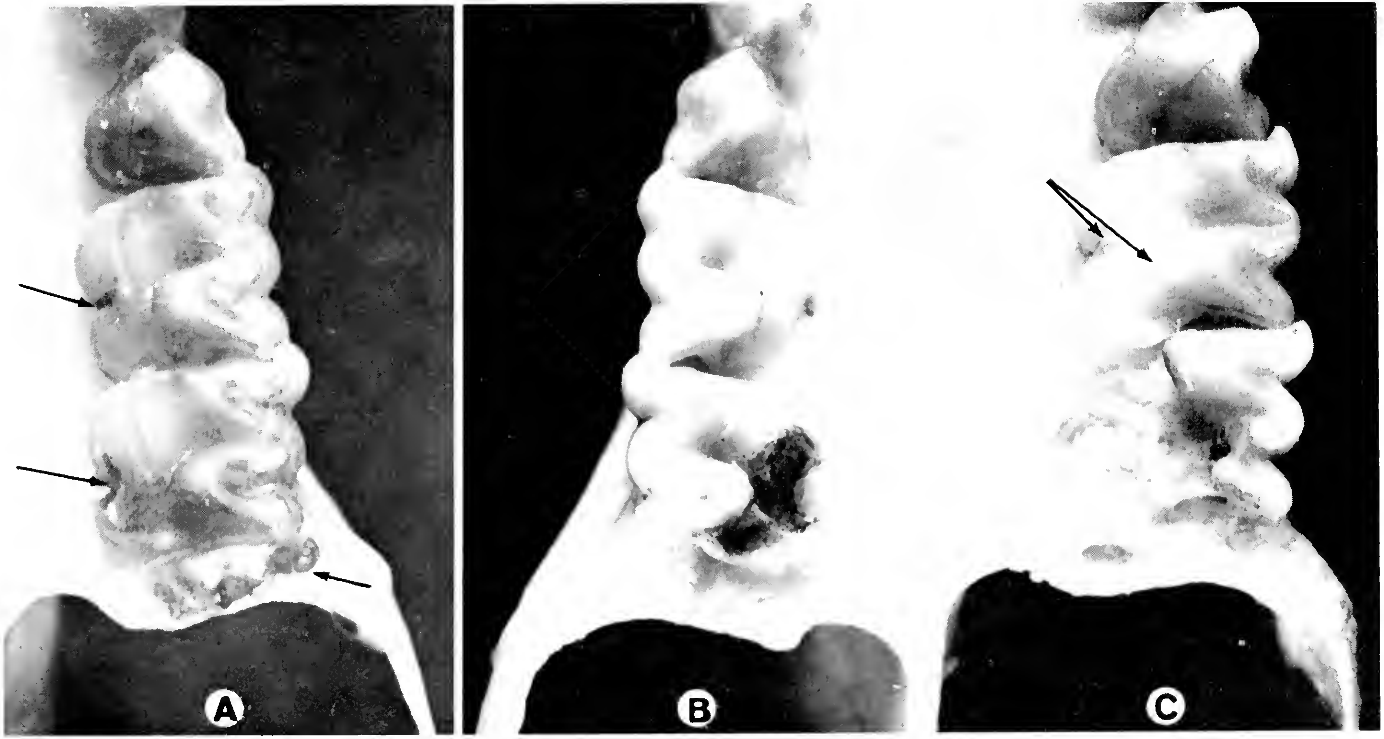

Fig. 1. Examples of dental caries in the upper molars of three different specimens of *P. hastatus*: (A) early stage of caries (arrows on left point out lesions in buccal pits of the first and second molars and arrow on right points out extensive lesions on third molar); (B) loss of third molar and destruction of part of the second; (C) loss of third molar and half of second molar (arrows indicate stained fissures on first molar).

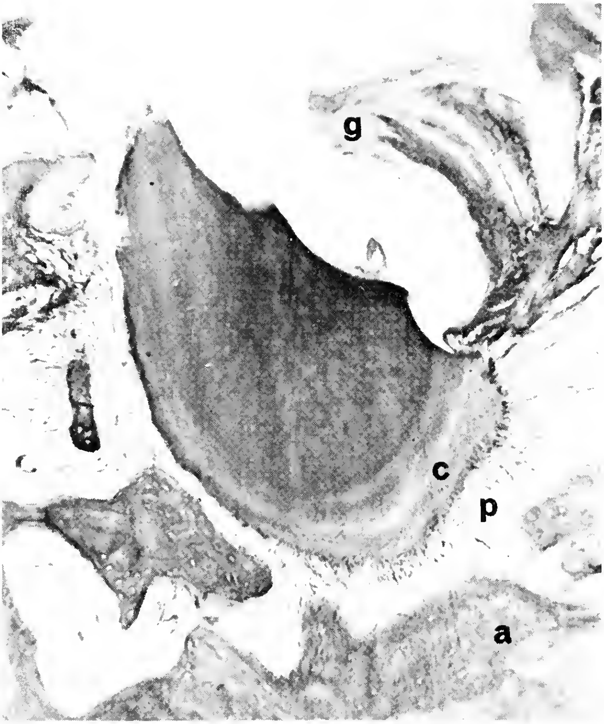

FIG. 2. Longitudinal section of carious (and now nonfunctional) upper premolar in *P. hastatus*. New layers of cement (c) have been added to the root of the traumatized tooth and principal fiber bundles of the periodontal ligaments (p) have been destroyed. Other lower case letters denote the alveolar bone (a) and gingiva (g). Stained with Mallory's triple.

Carious lesions in teeth of *P. hastatus* are found at certain sites, which are listed here in approximate order of importance based on incidence and severity of lesions: (1) the labial and posterior surface of the third upper molar; (2) the internal margin (entocristid to entoconid) of the talonid of the third lower molar; (3) the buccal pit anterior to the hypocone on the first and second upper molars; (4) the depression in the cingular shelf posterior to the metacone on the first and second upper molars, and (5) the site of intersection of fissures at the base of the metacone in these teeth; (6) the slight depression on the posterior medial surface of the upper incisors; (7) the depression on the surface of the cingular shelf of the upper canines; and (8) the crevice between the entoconid of one lower molar and the paraconid of the next. Generally, the sites of the most extensive carious lesions are characterized by a depression in the enamel and therefore are places where the surface is not subject to self-cleaning.

The enamel of teeth of *P. hastatus* typically is scored with stained fissures (Figs. 1, 3). The edges of some fissures can be detected with a sharp probe.

but we did not consider them carious unless we could detect a definite lesion in the enamel. Frequently, several fissures intersect in the same pit or depression. Such combinations of fissures and depressions provide an ideal site for penetration of the enamel (Fig. 3). This is especially true because the fissures extend through the enamel and into the dentin, appearing under the microscope as V-shaped wedges that can be traced along the surface of a tooth, at the dentino-enamel junction, in serial sections (Fig. 4). No relationship was found in *P. hastatus* between amount of wear on teeth and numbers of stained fissures. Some individuals with numerous stained fissures had only slight to moderate wear and others, having almost no fissures, also had moderately worn teeth.

The teeth of *Phyllostomus discolor* and *P. elongata* are strikingly different morphologically from those of *P. hastatus* at the very sites where most carious lesions occur in the latter. The most extreme modification is seen in *P. discolor*, which lacks the depressions that commonly are sites of infection in *P. hastatus*. It is of additional interest that fissure lines seldom are found on teeth of *P. discolor* and *P. elongata* and, when present, only rarely exceed one fissue per tooth. The teeth of *P. hastatus* are, overall, considerably more primitive than those of either *P. discolor* or *P. elongata*. Furthermore, the later two species differ considerably in size from *hastatus* in that they are much smaller.

In summary, carious lesions on the teeth of *P. hastatus* can be correlated with three endogenous factors of apparent cariogenic importance: (1) depressions on the surface of certain teeth, (2) numerous fissures in the enamel of teeth, often extending into the dentin, and (3) a flap of tissue that covers the labial coronal and cervical surfaces of the third upper molars. We are, of course, unable to judge the effect of the exogenous factors and the oral environment. The endogenous factors found in *P. hastatus* either are absent or are present to a much lesser degree in *P. discolor* and *P. elongata*. This and the apparent lack of dental caries in the latter two species does not prove, however, that *P. discolor* and *P. elongata* are somehow resistant to caries, because apparent resistance can result from the partial or total lack of exogenous cariogenic factors rather than the absence of endogenous factors (Dirks, 1965; Darling, 1965). In this regard, it is especially interesting that males of *P. hastatus* have a higher incidence of the disease than do females. We presently have no explanation of this phenomenon because we were unable to find any morphological difference in the teeth between the sexes. This discrepancy may be due to our small sample sizes.

The relationship between the occurrence of carious lesions and fissures and depressions in the enamel has been studied both in man and in laboratory rodents. Hunt and Hoppert (1950), for example, correlated broad fissures in teeth of rats with known susceptibility to caries; the broad fissures

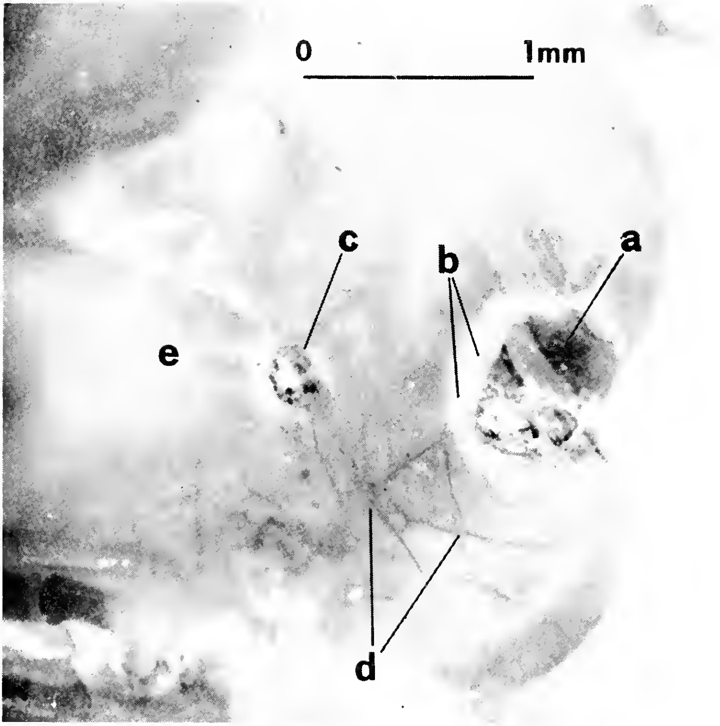

Fig. 3. Second upper molar of *P. hastatus*, showing exposed dentin in relatively small carious lesions (a and c), stained fissure lines extending through enamel (b), and stained fissure lines intersecting on the surface of the tooth (d). The metacone (not in focus) is labeled (e) for reference.

were thought to allow a greater chance for frequent impaction of food. In man, according to Dirks (1965), resistance to caries in individual teeth is lowest in pits and fissures and highest on free, smooth surfaces. This, of course, agrees with our conclusions about *P. hastatus*. Some workers (for example, Brucker, 1944) have debated the importance of fissures, but their arguments probably do not apply here because most were concerned with the problem of clinical diagnosis in man. The cause of the fissures that can be seen on teeth of *P. hastatus* is as yet unknown. It is possible that structural deficiencies in the dentin or enamel, or incomplete mineralization, allow for fissures to form along lines of stress. Because number of fissures does not appear related to wear, or to sites of surface depressions, it is doubtful that occlusion alone is responsible for the production of these barely macroscopic cracks (Fig. 3).

Feeding habits sometimes can be correlated with the incidence of dental caries. Hall (1940), for example, thought that diet played an important role in the production of caries in the teeth of bears. The dietary factor in

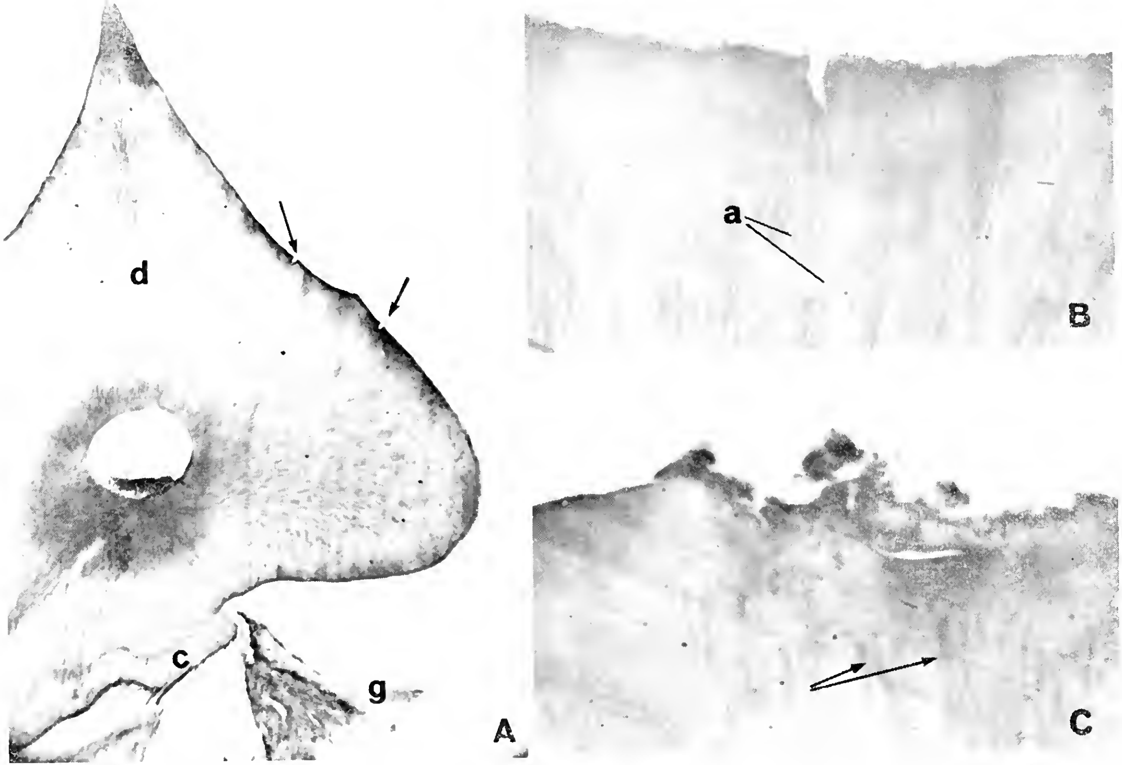

FIG. 4. Longitudinal sections of third upper molar of *P. hastatus*. A. Two conspicuous fissures extending into dentin (marked with arrows) on posterior surface of crown (enamel decalcified in preparation). B. View at higher power showing fissure and normal (air-filled) dentinal tubules (a). C. High-power view of a carious lesion; arrows indicate dead tracts in the dentin. All sections stained with Mallory's triple.

dental caries in *Phyllostomus hastatus* is unknown, but it might prove noteworthy that this species is known to feed on certain small vertebrates as well as on insects and fruit, whereas *P. discolor* apparently feeds on fruit and possibly also insects (Goodwin, 1946:307; Goodwin and Greenhall, 1961:238; Arata *et al.*, 1967). It is possible that mastication of certain kinds of food is one factor related to the formation of fissures in the enamel of teeth of *P. hastatus.* Dunn (1933) reported that captive spear-nosed bats easily crushed the bones of mice and small bats, which were readily eaten and possibly preferred to fruits.

Although all of the endogenous and exogenous cariogenic factors certainly cannot be determined at this time, it is noteworthy that acute dental caries occur commonly in *P. hastatus.* The occurrence of the disease and the phenotypic dental characteristics with which it is associated in this species suggest speculation in terms of their evolutionary significance. Two possible interpretations of the occurrence of caries in *P. hastatus* are: (1) one or more of the genetic factors that result in a high degree of acute dental caries are associated with some characteristic(s), for example large size, that is of significant survival value; (2) some exogenous factors, such as a recent (in an evolutionary sense) shift in food habits, are of great cariogenic import, and selection has not yet produced a phenotype capable of ameliorating these environment-produced conditions, or that the adaptive value of exploitation of a new food source is of far greater benefit to the species than prevention of dental caries. It might be argued, of course, that dental caries are not particularly important to the survival of an individual bat, but this seems unlikely when one considers that in severe cases of the disease entire teeth are lost and the gingivae undoubtedly are infected and inflamed. Future ecological and laboratory studies of all species of the genus *Phyllostomus* could shed additional light on the reasons for a high incidence of dental caries in *P. hastatus.*

Financial support for this study was from a contract (DA-49-193-MD-2215) with the United States Army Medical Research and Development Command and a grant (3453-5038) from The University of Kansas General Research Fund. Richard G. Van Gelder and Karl F. Koopman, The American Museum of Natural History, kindly loaned us specimens of *Phyllostomus elongata* and James W. Bee and G. Lawrence Forman, The University of Kansas, helped us with certain aspects of histological studies.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVIII Pages 801-844 May 1, 1970 No. 21

The Skeleto-Muscular System of Mecoptera: The Thorax[1,2]

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ABSTRACT

This is the second of a series of morphological studies on the order Mecoptera, and treats the thoracic skeleton and musculature. The cervix is well developed and is unique among all orders in the possession of musculated dorsocervicalia. The prothorax generally tends toward reduction and fusion of sclerites, especially in the lateroventral field; however, the prothoracic musculature is fairly constant despite skeletal variations. The pterothoracic segments are extremely generalized in both sclerite arrangement and in musculature but certain modifications do accompany brachyptery and aptery. The tendency toward involution of the sternum resulting in cryptosterny reaches an extreme condition in Mecoptera, where there is no longer any external evidence of a sternum. The normal articulations of the legs with the thorax are more restricted in Mecoptera than in other orders; i.e., the trochantinocoxal articulation is absent and there is no involvement of the meron in the coxopleural articulation of the mesothoracic leg. The pterothoracic musculature is constant in most cases but some variation does occur in the pleural series. With the exception of raptorial modifications in one family, the legs of Mecoptera are extremely generalized.

INTRODUCTION

This investigation of the thorax is one of a series of morphological studies on the order Mecoptera (Part 1, Hepburn, 1969). Two priorities underlie the approach used in this paper. The first is that a basic knowledge of the thoracic skeleton and musculature was needed for the order as a whole. The second is that once such information was obtained, a more critical study could then be made of the Panorpoid Complex. Only the first of these problems is treated here, except for a few comments on the musculature with reference to other orders.

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The thoracic morphology of Mecoptera has received little notice in the past; however, the few papers which do treat the order are outstanding. The principal pertinent work was that of Hasken (1939) who discussed the thoracic skeleton and musculature of Panorpidae in detail. Issiki (1933) studied the exoskeleton of Panorpidae and Panorpodidae; Maki (1938), the musculature of Panorpidae; Ferris and Rees (1939), the skeleton of Panorpidae. More recent work includes excellent papers on Boreidae (Fuller, 1954, 1955), the exoskeleton of Meropeidae (Mickoleit, 1967), and the pleurosternal musculature of the Panorpoid Complex (Mickoleit, 1969).

Historically, the paper by Hasken and that of Ferris and Rees assume importance in morphology beyond the scope of Mecoptera anatomy. These authors, especially the latter, were among the first to interpret the thoracic sternum of Mecoptera in terms of the cryptosterny thesis of Weber. This view, which has been adopted in this paper, has been further advanced by Matsuda (1960, 1963a,b) in his comparative study of the insect pterothorax.

Other problems related to the thoracic skeleton include structural discrepencies between the prothoracic and pterothoracic pleural regions, the modifications of this region through reduction to brachyptery and aptery in Boreidae and Apteropanorpidae, and the nature of the coxal articulations. The role of the mesothoracic meron in the coxopleural articulation is unique in Mecoptera. The thoracic tergum is straightforward and offered no special problems.

The muscular system ordinarily would have included the problem of homologizing the muscles of the three segments but this is worked out by Hasken (1939). Hasken's work is used as a standard of comparison for all of the other families. The loss of muscles in the flightless forms presents no special problems of interpretation. The thoracic musculature of Mecoptera is in some instances compared with that of other orders of the Panorpoid Complex by reference to the tables given by Maki (1938).

Terminology remains a problem central to insect morphology and one is caught between following an existing nomenclature with faults as opposed to modifying it or coining a new one. The former course is taken in this paper. Two different systems of terminology are used in this paper. The terminology applied to the skeletal region is based on Snodgrass (1927, 1935) with refinements by Matsuda (1960). The terminology applied to the musculature is that of the "European system" used by Hasken (1939) and Fuller (1955) in which more emphasis is placed on a consistent classical name than implying functional significance. This system was followed here both because it facilitates an easy comparison of all of the literature on the thoracic musculature of Mecoptera and because this study is not a functional analysis of the musculature.

ACKNOWLEDGMENTS

I would like to credit Dr. George W. Byers for his interest and support of this project, Dr. C. D. Michener and R. W. Lichtwardt, all of the University of Kansas for a review of the manuscript; Dr. C. O. O'Brien and Dr. L. B. O'Brien for collecting much of the material used in this study.

METHODS AND MATERIALS

The specimens employed in this study are representative of all nine families of Mecoptera currently recognized in the classification of Byers (1965). The justification for the selection is expressed in the first part of this study (Hepburn, 1969) on the skeleto-muscular system of the head. The species used and their classification are as follows:

- Panorpidae
  - *Panorpa nuptialis*
  - *Panorpa communis* (from the literature)
  - *Panorpa lugubris*
  - *Panorpa sibirica*
  - *Neopanorpa harmandi*
- Bittacidae
  - *Bittacus chlorostigma*
  - *Bittacus italicus* (from the literature)
  - *Bittacus pilocornis* (from the literature)
  - *Bittacus strigosus* (from the literature)
  - *Apterobittacus apterus*
  - *Harpobittacus australis*
  - *Harpobittacus tillyardi*
  - *Pazius obtusus*
  - *Anabittacus iridipennis*
  - *Kalobittacus microcerus*
  - *Austrobittacus anomalus*
  - *Neobittacus blancheti*
- Apteropanorpidae
  - *Apteropanorpa tasmanica*
- Choristidae
  - *Chorista australis*
  - *Taeniochorista pallida* (from the literature)
- Meropeidae
  - *Merope tuber*
- Boreidae
  - *Boreus unicolor*
  - *Boreus californicus*
- Nannochoristidae
  - *Nannochorista dipteroides*
  - *Nannochorista maculipennis*
- Notiothaumidae
  - *Notiothauma reedi*
- Panorpodidae
  - *Panorpodes paradoxa* (from the literature)
  - *Brachypanorpa carolinensis*

Fluid-preserved specimens (70% ethanol, Bouin's soln., Kahle's soln., or Dietrich's soln.) were dissected in 70% ethanol, with razor blade fragments and jewelers' forceps, under a standard dissecting microscope. Occasionally the tissues required histological staining to accentuate certain features of skeleton and musculature. After initial dissection, specimens were placed in a 0.5% solution of Congo red and 70% ethanol for 30 minutes, washed in 70% ethanol and then examined. The residual effect is that the stain partially washes out of the muscles but is retained by the endoskeleton. This greatly facilitated locating origins and insertions of muscles. A solution of 0.5% methylene blue in 70% ethanol was also used for high-lighting muscles, but this stain has no residual effect.

The external skeletal morphology was examined in several ways. In some instances pinned specimens were sufficient (and in some cases were the only ones available) to yield gross information. Fine details of external structure and the details of internal skeletal structure were usually elucidated by boiling the specimen in a 10% KOH solution and washing in 70% ethanol. After such treatment the specimens are often too hyaline to discern fine elements, and the specimen must then be stained. Again, Congo red proved useful. If a specimen is first stained in Congo red, washed, and then boiled in a 10% KOH solution, the soft tissues are rendered while the cuticle retains the stain perfectly. In those specimens which were not boiled but simply stained for muscle work, the residual stain was particularly concentrated along apodemes and apophyses, presumably owing to chemical differences in these areas. No attempt was made to identify the cuticular layers, but this reaction is useful in following apodemes.

Where possible, drawings were made after the examination of several individuals to avoid being misled by teratological specimens. The illustrations were made by use of an ocular grid and grid paper.

LIST OF ABBREVIATIONS

a	apodeme
aa	anterior apodeme
ab	abdomen
ac	anapleural cleft
acs	antecostal suture
aes	anepisternum
ar	arolium
as	anapleural suture
awp	anterior notal wing process
ax	auxillia
b	basalare
bas	basisternum
bc	basicosta
bs	bsasalar suture
dc	dorsocervicale
ec	eucoxa
em	epimeron
ep	episternum
fa	furcal arm
fs	furcasternum
fu	furca
ic	intrasegmental conjunctiva
ks	katepisternum
ke	laterocervicale
lec	lumen of eucoxa

lpn	lateropostnotum
m	meron
pa	pleural apophysis
pca	pleuro-coxal articulation
pcs	precoxal suture
pes	preepisternum
ph	phragma
pla	pleural apodeme
pln	planta
poa	posterior apodeme
pon	postnotum
ps	pleural suture
pt	pretarsus
pwp	posterior notal wing process
s	spiracle
sb	subalare
sca	sterno-coxal articulation
scl	scutellum
sct	scutum
sl	scutal lobe
sr	sternal ridge
tn	trochantin
trt	trochanteral tendon
$ts_{4 \ldots 5}$	tarsomere
u	unguis
up	unguitractor plate

CERVIX

There have been only two comparative treatments of the insect cervix, those by Verhoeff (1903) and by Crampton (1926). Since the ontogenetic development of the cervix has yet to be studied in detail, it is not known to what extent cephalic and thoracic elements contribute to its formation in most instances. The cervix is included with the thorax in this paper for two reasons, tradition and the fact that several cervico-thoracic muscles point to a more intimate relationship with the thorax than with the head. Nevertheless, the inclusion of the cervix with a discussion of the thorax should be taken as arbitrary and not in any way as an espousal of the old "microthorax" theory (Snodgrass, 1909).

The cervix or neck of Mecoptera is, as in other insects, a mostly membranous area between and joining the head and prothorax. In most insects it is a small and inconspicuous region, but in Mecoptera it is quite extensive. It includes a variable number of sclerites: a pair of usually lateral laterocervicalia (lc, Figs. 5, 7-9, 19, 22) and occasionally a pair of dorsal dorsocervicalia (dc, Fig. 24). A pleural element, the trochantin, lies within the ventral cervical field, but it is not functionally related to the other sclerites of the neck. Not only is the structure of each of these elements variable, but the entire complex bears a close relationship to the prothorax and varies with prothoracic development. Each of these elements is considered separately.

The degree to which the dorsum of the cervix is membranous varies with the anterior extent of the pronotum. In Meropeidae, Boreidae, and Bittacidae the anterior edge of the pronotum extends to and covers the base of the head. The Panorpidae and Apterpanorpidae exhibit the most extensive cervicoria, hence the smallest relative pronotal size. The remaining families are intermediate. Considering the first case (the first three families mentioned), a consequence of pronotal enlargement has been a lateroventral displacement of the laterocervicalia: a) in Meropeidae the laterocervicalia have become entirely ventral and extend parallel to the longitudinal axis of the body (Mickoleit, 1967); b) Boreidae are the same but, in addition, the pronotum has extended laterally and anteriorly such that the posterior bases of the laterocervicalia have been shifted forward, with the result that they lie in a dorsoventral plane perpendicular to the long axis of the body (Fuller, 1954); c) in Bittacidae the laterocervicalia are in the generalized position but are not externally visible because they are obscured by the lateral swelling of the pronotum.

In the intermediate forms (Notiothaumidae, Fig. 24; Panorpodidae, Fig. 19 and Issiki, 1933; Choristidae, Fig. 23; and Nannochoristidae, Crampton, 1926) the relationship of pronotum and laterocervicalia is the usual one, the laterocervicalia extending obliquely from prothorax to postocciput in a longitudinal direction (with the exception of Nannochoristidae in which they extend dorsoventrally). In Panorpidae (Hasken, 1939) the Apteropanorpidae (Fig. 22), the pronotum is reduced and the laterocervicalia occupy a generalized position.

LATEROCERVICALIA

The most persistent cervical slcerties of insects generally, and more specifically of Mecoptera, are the laterocervicalia. In general, the laterocervicale is a long, narrow sclerotic process which articulates anteriorly with the head at the occipital condyle and posteriorly with the propleuron. The laterocervicale is incised by a suture for most of its length. Internally a well developed apodeme is formed along the suture and serves as a site for muscle attachment. Although the anterior articulation with the occipital condyle is constant, the relationship of the laterocervicale with the propleuron is variable. In the majority of families the laterocervicale is produced into a process which articulates with the propleuron (usually the proepisternum, but in some instances the propleurites are fused and so reduced that it it not possible to distinguish which propleurite is involved). The exceptions are the Notiothaumidae and Panorpidae, in which the laterocervicale is basally fused with the propleuron (Fig.2) and the Bittacidae in which the single propleural sclerite is longitudinally fused with the long axis of the laterocervicale.

Dorsocervicalia

In addition to the laterocervicalia, some families of Mecoptera possess a pair of transverse, oblong dorsal sclerites of the cervix situated immediately behind the postocciput, the dorsocervicalia (dc). These sclerites are present in Panorpidae, Boreidae, Notiothaumidae, and Panorpodidae (only in the Asian *Panorpodes*). Their occurrence in Mecoptera is unusual in that they serve as sites for muscle attachment, which is not typical of these sclerites in other insects (Snodgrass, 1935).

In those Mecoptera with dorsocervicalia, the dorsal longitudinal muscles extend from the first phragma and terminate on the posterior edges of the dorsocervicalia, while those familes lacking dorsocervicalia have the anterior termination of these muscles on the postoccipital ridge. There are several explanations for these differences, the most plausible of which is that the dorsocervicalia arose by fragmentation from the original postocciput. Although there is no available evidence from development studies, this view appears more acceptable than a *de novo* origin of dorsocervicalia.

Crampton (1926) adequately discusses the skeletal anatomy of the mecopteran cervix as it relates to the other orders of the Panorpoid Complex; he illustrates several examples of the mecopteran cervix. Issiki (1933) and Hasken (1939) discuss Panorpidae. Ferris and Rees (1939) in their study of Panorpidae incorrectly suggest that the dorsocervicalia are unique to Mecoptera.

Cervical Musculature

The musculature of the mecopteran cervix was first elucidated by Hasken (1939) for Panorpidae; this work is used as a standard of comparison for the musculature of the cervix and thorax of other Mecoptera. The presence or absence of muscles is tabulated by families (Tab. I), although variations are discussed separately.

Intersegmental Muscles

longitudinal muscles (Fig. 2)

Odlm$_1$. Anterior side of phragma 1 at the midline to the dorsocervicale or the postoccipital ridge. In those families with dorsocervicalia, the insertion is on the posterior side of the sclerite; in those lacking dorsocervicalia, the insertion is on the postoccipital ridge. This muscle elevates the head.

Odlm$_2$. Middle of the pronotum to the dorsocervicale or occipital ridge; retracts the cervicorium, and the resulting creasing facilities the antero-posterior movement of the head.

Ovlm$_1$. Anterior side of the profurca near its middle to a small tendon on the lateral arm of the tentorium; depressor of the head in conjunction with the next muscle.

Table 1. Cervical Musculature.

	CHORISTIDAE	NANNOCHORISTIDAE	BITTACIDAE	PANORPODIDAE	PANORPIDAE	BOREIDAE	MEROPEIDAE	NOTIOTHAUMIDAE	APTEROPANORPIDAE
Odlm$_1$	+?	+	+	+	+	+	+	+	+
Odlm$_2$	−?	−	−	−	−	+	−	+	−
Ovlm$_1$	+?	+	+	+	+	+	+	+	+
Ovlm$_2$	+?	+	+	+	+	+	+	+	+
Oism$_1$	+?	−	−	+	+	+	−	+	+
Oism$_2$	+?	+	+	+	+	+	−	+	+
Oism$_3$	+?	−	+	+	+	+	−	+	+
Oism$_4$	+?	+	+	+	+	−	−	+	+
Oism$_5$	+?	−?	+	+	+	+	−	+	+
Odvm$_1$	+?	+	+	+	+	+	+	+	+
Odvm$_2$	+?	+	+	+	+	+	+	+	+

Ovlm$_2$. Immediately ventrad of Ovlm$_1$ and has the same insertion and function as Ovlm$_1$.

OBLIQUE MUSCLES (Fig. 2)

Oism$_1$. Junction of the profurca and the propleuron to a short tendon either on the lateral edge of the dorsocervicale or on the postoccipital ridge near the insertion of Odlm$_1$; elevates the head.

Oism$_2$. Laterally on the anterior pronotal furrow to the dorsal side of the laterocervicale; elevates the laterocervicale. Indirectly effects movement of the head.

Oism$_3$. Laterally on the base of phragma 1 to the laterocervicale between the insertions of Oism$_2$ and Oism$_4$; with Oism$_2$ it elevates the anterior end of the laterocervicale.

Oism$_4$. Anteroventrally of Oism$_1$ to a short tendon on the laterocervicale; elevates the laterocervicale.

Oism$_5$. Basicosta of the procoxa to the anteroventral end of the laterocervicale; indirectly elevates the head.

Segmental Muscles

DORSOVENTRAL MUSCLES (Fig. 2)

Odvm$_1$. Dorsal side of the laterocervicale to either the dorsocervicale or the postoccipital ridge; elevates the head.

$Odvm_2$. Immediately behind $Odvm_1$ on the dorsal side of the laterocervicale to either the posterior end of the dorsocervicale or the postoccipital ridge; elevates the head.

PROTHORAX: PRONOTUM

The pronotum of Mecoptera is in general a heavily built sclerite that is extensive both dorsally and caudoventrally. Anteriorly it may overlap the vertex (see cervix) and laterally the propleurites. It is produced caudoventrally into a tapered process which is connected by a hinge to the mesepisternum at its apex. Very rarely the process is continuous with the mesepisternal spur; i.e., in *Panorpa sibirica* as reported by Issiki (1933) and confirmed by me. Thus Hasken's criticism (1939) of Issiki on this point is unjustifiable.

The pronotum is creased by longitudinal and transverse furrows, some of which internally produce apodemes for muscle attachment. Since these furrows are not sutures in the classical sense (no apodemes), Miyake's attempt (1913) to homologize the resulting subdivided areas with pterothoracic sclerites related to flight is unacceptable, as pointed out by Hasken (1939) and Snodgrass (1935). The first furrow simply traverses the pronotum; the second sets off a protuberance on either side of the midline; the third begins on the protuberances and extends into the caudoventral process at the mesepisternum, serving internally as a site for muscle attachment (*$Odlm_2$* and *$Oism_2$*). Likewise, the first furrow bears an apodeme for muscle attachment (*1dlm*). This constitutes the generalized case in Mecoptera to which the majority of families correspond.

The development of the lateral process of the pronotum (aw, Figs. 19-21, 23, 24) varies from a well produced arm in Notiothaumidae to a very reduced one in Apteropanorpidae, Boreidae, and Bittacidae, the other families being intermediate. However, the internal apophysis of this arm is the site of attachment of the *1dvm* muscle in all families of Mecoptera. The internal development of the furrows is also variable. In some families (Apteropanorpidae, Boreidae, and Bittacidae) there are only slight indications of apodemes; in others (Notiothaumidae) a well developed apodemal ridge extends from one side of the pronotum to the other. The number of pronotal apodemes varies from 0 to 2. Apteropanorpidae are unique in having a single external furrow and no apodemes; in addition, the first thoracic spiracle is completely imbedded in the posterior part of the pronotum and not in the membranous region behind the lateral process (aw) of the pronotum (also in Boreidae). Besides transverse furrows, the Meropeidae possess a longitudinal apodeme and a short process in the lateral wall of the pronotum, both parallel to the long axis of the body (Mickoleit, 1967). Since there is no consistent plan of development in the prothorax of insects (Snodgrass, 1935) it is difficult to make phylogenetic inferences here, and by extension difficult to assess variation found in the pronota of Mecoptera.

PROTHORAX: Propleuron

The propleuron of Mecoptera contains both of the sclerites usually associated with this region—the proepisternum and proepimeron. Externally the propleuron is situated below the pronotum and dorsal to the coxal bases. Because of the extensive cervicoria, the propleuron is posteriorly displaced such that a portion of it is concealed by the cervical membrane and the lateral extension of the pronotum. At the anterior end of the propleuron there is a transverse apodemal process which extends to the furca. Internally the proepisternum extends caudally (though externally obscured by cervicorium and pronotum) to the furca.

The proepimeron is situated immediately behind the proepisternum and is extremely reduced. However, the two propleurites are separated from each other by a suture (probably corresponding to the pleural suture) at the ventral end of which is an apophysis. The junction of propleuron and furca is represented by a fusion of proepimeron, profurca, and pleural apodeme, and only a vestige of the proepimeron is recognizable in most cases. That the proepimeron is present as part of the fusion product is indicated by the attachment of the dorsoventral intersegmental muscle *(Iism)*.

The proepisternum articulates anteroventrally with the laterocervicale and posteroventrally with the base of the coxa which comes to a point.

The epimeron continues ventrally into the depression of the furca, posterior to the episternum. Anteriorly there is a process of the furca which serves for muscle attachment. The monocondylic articulation of the procoxa with the proepisternum is unique and in contrast to the dicondylar state of the pterothoracic coxae, in that the procoxal connection with the episternum is immovable while those of the latter are not (Hasken, 1939).

As indicated by Snodgrass (1935), the propleurites of insects are always separated into episternum and epimeron, though the latter tends toward reduction. This is true of Mecoptera and has been verified (various authors) and confirmed by me. Crampton (1926) claimed that there is a tendency for fusion of laterocervicalia and propleuron in Mecoptera based on an approximate condition in Choristidae and on an actual fusion in *Panorpa lugubris* (Panorpidae). A close examination of Panorpidae (including *P. lugubris*) does not support this claim. In fact, there is no fusion between the laterocervicalia and propleurites in any of the Mecoptera examined in this study.

The propleural elements anterior to the pleural suture are termed the precoxale or precoxal bridge, an extremely reduced area in the prothorax of Mecoptera. The only remnant of a coxolpleurite in Mecoptera is a very reduced, isolated, ventral trochantin. In the lower Pterygota this sclerite is derived from the primitive coxopleurite (Snodgrass, 1935) and usually articulates with the coxa as well as serving as a site for muscle attachment of tergal promotor muscles. In the higher Pterygota the trochantin becomes reduced, as in all Mecoptera. The trochantin of the prothorax does not receive any muscles nor does it articulate with the procoxa. A trochantin is present in the prothorax of all Mecoptera, though Evans (1942) claimed the contrary.

Issiki (1933) adequately discussed the trochantin and interpreted it correctly in Panorpidae and Panorpodidae, as did Ferris and Rees (1939) in Panorpidae. Other cited papers on Mecoptera make no mention of this sclerite.

PROTHORAX: PROSTERNUM

Discounting minor variations in shape and size, the prosternal field is uniform in its constituents. The basic structure closely approximates that of the generalized lower Pterygota (Snodgrass, 1935). The only sternal intersegmental element, the spinasternum, is intimately fused with the prosternum and is externally visible as a reduced spike-like caudal process of the furcasternum (or sternellum). Internally it is produced into an apophysis to which are attached the ventral longitudinal intersegmental muscles *(1vlm)* that extend from the mesothorax into the prothorax. Snodgrass (1935) reports that there are occasionally two such spinasternal elements in insects; there is one on either side in Mecoptera.

The sternal elements in the prothorax of Mecoptera include, in an anteroposterior direction: a eusternum, apophyseal pits (or furcacavae), and a spinasternum. There are no pleurosternites in the prothorax. The eusternum is generally triangular to trapezoidal and is wedged between the bases of the closely appressed coxal bases. Its anterior basisternum (bs) and posterior furcasternum (fs) are externally divided by a Y-shaped sternal suture (in most other insects this is a simple transverse suture). The furcal pits are posterolateral on the eusternum and give rise to an extensive sternal apophysis which forms the major endoskeletal element of the prothorax. The degree of sternal involution has obliterated the sternacostal suture and sternacosta seen in other insects. The position of the furcal pits partially delimits the basisternum and furcasternum. The sternal apophyses are mesally fused and at the level of the base of the procoxae they branch laterally into an anchor-shaped process continuing to the pleuron, where they fuse with the pleural apophyses, as well as serve as sites for muscle attachment (see propleuron).

Compared to generalized Pterygota (i.e., of the Orthopteroid level) the Mecoptera have an extremely involuted prosternum that exhibits a trend toward fusion of the elements into a single undifferentiated sclerite, as evidenced by the fusion of the spinasternum with the furcasternum, the appression of basisternites and furcasternites of either side into a single unit, lack of a strenacostal suture and sternacosta, and the extreme development of the endoskeletal furca within the prothorax. Inasmuch as the sternum of the prothorax is homodynamous with that of the pterothorax, the trend is further borne out in the latter in which sternal involution is complete and the development of the furca reaches an extreme among insects.

Gross descriptions of the prosternum are available for Boreidae (Fuller, 1954, 1955), Meropeidae (Mickoleit, 1967), and Panorpidae (Hasken, 1939). Although Crampton (1926) illustrated three families, his discussion is nebulous. Issiki (1933) discussed the prosterna of Panorpidae and Panorpodidae. My own findings and interpretations parallel his. The prothoracic leg is discussed with the pterothoracic legs.

PROTHORACIC MUSCULATURE

The musculature of the prothorax was first worked out in Panorpidae by Hasken (1939). As with the cervical muscles, those of the prothorax are compared, with Hasken as a standard; the presence or absence of muscles is listed in Table 2.

Intersegmental Muscles

LONGITUDINAL MUSCLES (Figs. 2, 25)

1dlm. Mesonotum at the base of phragma 1 to the apodeme of furrow 2 or 3 of the pronotum; effects a close appression of pronotum and mesonotum.

1vlm. Posterior side of the profurca anteriorly and somewhat obliquely to a long tendon on the anterior side of the mesofurca; effects appression of pro- and mesosterna. This muscle is subdivided into $lvlm_1$ and $lvlm_2$ in Notiothaumidae but in no other families.

OBLIQUE MUSCLES

1ism. A projection of the caudal aspect of the proepimeron to the mesonotum behind $Oism_3$; maintains the position of the propleuron.

Segmental Muscles

DORSOVENTRAL MUSCLES

1dvm. Posterolateral edge of the pronotum to the inner edge of the merocosta. It is laterad of lism and posterior to the pleurocoxal articulation; a remotor of the coxa.

INTRAFURCAL MUSCLES

1ifum. Between the arms of the furca; antagonistic to the strenal leg muscles by drawing the furcal arms toward each other.

TABLE 2. Prothoracic musculature.

	CHORISTIDAE	NANNOCHORISTIDAE	BITTACIDAE	PANORPODIDAE	PANORPIDAE	BOREIDAE	MEROPEIDAE	NOTIOTHAUMIDAE	APTEROPANORPIDAE
1dlm	+?	+	+	+	+	+	+	+	+
1vlm	+?	+	+	+	+	+	+	+	+
1ism	+?	+	—	+	+	+	+?	+	—?
1dvm	+?	+	+	+	+	+	+	+	+
1ifum	+?	—	+	+	+	+	+	—?	+
$1pm_1$	+?	+	+	+	+	+	+	+	+
$1pm_2$	+?	+	+	+	+	+	+	+	+
$1pm_3$	+?	+?	+	+	+	+	+	+	+
$1pm_4$	+?	+?	+	+	+	+	+	+	+
$1bm_1$	+?	+	+	+	+	+	+	+	+
$1bm_2$	+?	+	+	+	+	+	+	+	+
$1bm_3$	+?	+	+	+	+	+	+	+	+
$1cxm_1$	+?	+	+	+	+	+	+	+	+
$1cxm_2$	+?	+	+	+	+	+	+	+	+
$1cxm_3$	+?	+	+	+	+	+	+	+	+
$1cxm_4$	+?	+	+	+	+	+	+	+	+

PLEURAL MUSCLES

1pm$_1$. Dorsal side of the episternum and to the basicosta between the pleuro-coxal hingle and Oism$_5$; a coxal promotor.

1pm$_2$. Dorsal side of the episternum behind 1pm$_1$ ventrally to the trochanteral tendon where it inserts; a femoral abductor.

1pm$_3$. Anterolateral part of the pronotum to the dorsal side of the propleuron where it joins a process of the pleural apodeme; maintains the position of the propleuron.

1pm$_4$. Dorsal side of the episternum to the apodeme of furrow 2 or 3 of the pronotum; in conjunction with 1pm$_3$ it maintains the position of the pleuron with respect to the notum since they connect the two sclerites. They are also antagonistic to 1pm$_1$ and 1pm$_2$.

Leg Muscles

STERNAL LEG MUSCLES

1bm$_1$. Inside of the sternum to the posterior side of the basicosta; a coxal promotor.

1bm$_2$. A projection of the anterior or ventral side of the profurca to the trochanteral tendon; a femoral abductor.

1bm$_3$. Ventral side of the furca to the basicosta, being disposed between the pleuro-coxal articulation and IIcxm$_1$; a coxal remotor.

COXAL MUSCLES

1cxm$_1$. Anterior surface of the coxa to the proximal end of the trochanter at the articulation between coxa and trochanter; a femoral adductor.

1cxm$_2$. Basicosta to the lateral proximal edge of the trochanter posterior to the termination of 1cxm$_1$; a femoral adductor.

1cxm$_3$. Posterior side of the coxa to the lateral proximal edge of the trochanter immediately posterior to 1cxm$_2$; a femoral adductor.

1cxm$_4$. Medial edge of the coxa to the medial side of the trochanteral tendon; a femoral abductor.

MESOTHORAX: Mesonotum

The mesothoracic tergum is of the generalized type described by Snodgrass (1927, 1935, etc.). Ferris and Rees (1939) pointed out that the thoracic terga of Panorpidae are of the textbook variety and offer no difficulty of interpretation. As a generalization, this is true of all Mecoptera; however, certain modifications do occur in those forms which approach aptery, in which there is a tendency towards consolidation of sclerites into a single indistinguishable plate (e.g., Apteropanorpidae, Fig. 22).

The mesonotum of Mecoptera is initially divisible into two plates, an anterior alinotum and a posterior postnotum. The alinotum is further subdivided into two plates, a large anterior scutum (sct) and a small posterior scutellum (scl) by the scuto-scutellar suture (scs), which is internally produced into a reenforcing apodeme (the "V-formige Leiste" of German authors, Figs. 1, 4, and 12). In most Mecoptera the alinotum and postnotum (pon) are separated by a membranous area of secondary intrasegmental conjunctiva (ic). In the higher Pterygota the tendency is for reduction of this conjunctival region in connection with more efficient and complex flight (Snodgrass, 1935), a modification possessed only by the Bittacidae among Mecoptera (Fig. 12). There is no comparative information available on the relative flight ability of various Mecoptera to assess the value of this modification, but Bittacidae appear to be the most accomplished flyers. This would at least circumstantially support Snodgrass' contention. This principle is well founded, however, with respect to insect flight in general (Pringle, 1957).

The anterior limit of the scutum is the antecostal suture (acs). This suture is also an indication of an invaginated phragma of two lobes, one on either side of the midline, to which the dorsal longitudinal muscles attach. Anterior to the suture is a very short sclerite, the acrotergite (precosta of Issiki, 1933), which is extremely reduced in Mecoptera and in other higher Pterygota (Snodgrass, 1935). Separate prescutum and parapsidal furrows do not occur in Mecoptera.

The convex scutum bears an anterior notal wing process or tergal lever (awp) as a flattened flanged process on either side (Figs. 1, 4, 12). This process is bilobed, with the anterior lobe slightly below the level of the posterior lobe. The first axillary sclerite articulate between the lobes. Hasken (1939) discussed these processes as distinct from each other but they collectively function as a single notal process. At the posterior end of the mesoscutum in most Mecoptera there is a slender, forked posterior notal wing process (pwp). The wing is connected to and articulates with the notum between these processes. The scutellum is variable in shape (oval to pentagonal), but in all cases it is laterally drawn out into a thin process on either side and is continuous with the axillary cord of the posterior edge of the wing.

The transverse postnotum is subdivided into a median portion (pon) and a quadrangular lateropostnotum (lpn) on either side. Ventrally the lateropostnotum ends on the dorsal edge of the epimeron. Posteriorly the postnotum is delimited by a transverse suture (acs), the antecostal suture of the next segment, that indicates the position of the next phragma and the end of the mesonotum. Anteriorly the scutum is separated from the episternum by a conjunctival area (Figs. 19-21, 23, 24).

This is a general account of the mesonotum of fully winged Mecoptera (Panorpidae, Panorpodidae, Choristidae, Nannochoristidae, Notiothaumidae, Meropeidae, and Bittacidae) and does not apply to brachypterous or apterous forms. Minor variations as width/length and degree of convexity can be seen by comparison of dorsal and lateral views illustrated (Figs. 4, 12, 19, 21, 23, 24). The Bittacidae are noteworthy in this group because 1) there are two large anterior scutal lobes which receive the tergosternal muscles; 2) the posterior notal wing process is simple, unforked; and 3) in some genera there is no secondary conjunctiva between alinotum and postnotum (Fig. 12).

The modifications of the mesonotum in Boreidae are discussed in detail by Fuller (1954). In addition to being brachypterous, males of Boreidae utilize their wings as accessories in mating, the details of which were described by Cooper (1940). In summary, the situation in Boreidae is that 1) the membranous areas of the tergal region have become enlarged, 2) the scutum, postnotum and lateropostnota are all reduced, as are the phragmata, 3) the scutum is medially divided by the anterior extension of the scutellum which is relatively large (i.e., the scuto-scutellar suture almost reaches the antecostal suture), and 4) the postnotum is anteroventrally produced below the scutellum. The net effect is that the notal sclerites are generally reduced and that all of the mesonotal sclerties have become anteroventrally displaced. The anterior and posterior notal wing processes are present but widely separated and apparently functionless. There is a strong sexual dimorphism in the mesonotum (Fuller, 1954).

The most extreme example of thoracic amalgamation and reduction is represented by the wingless Apteropanorpidae (Fig. 22). In this family all three of the thoracic nota and pleura are fused into a single saddle-shaped unit that is traversed by furrows. There is no trace of either dorsal longitudinal or tergal muscles so that it is difficult to interpret exactly what these furrows (sutures?) really represent. In the mesothorax there is a single transverse furrow which terminates at the coxal bases on either side. It is not possible to assign the demarcated areas to either alinotal or postnotal regions. There is no trace of a wing structure, associated sclerites, internal apophyses, or phragmata. Internally the furrows are represented by fine trace apodemes but there are no muscles associated with them.

In the two flightless bittacid genera, *Apterobittacus* (which is completely apterous) and *Anomalobittacus* (which is brachypterous), the thoracic segments are clearly distinguishable from one another; distinct notal and pleural regions are visible as well (Fig. 21). While there is some reduction, there is no fusion of the kind seen in Apteropanorpidae. There is no rearrangement nor superposition of sclerites as in *Boreus*, only a loss of those elements directly related to flight such as anterior and posterior wing processes and reduction of phragmata. Likewise, there are no tergosternal or dorsal longitudinal muscles in *Apterobittacus* (no specimens of *Anomalobittacus* were available for dissection).

METATHORAX: METANOTUM

The tergum of the metathorax is extremely similar in structure to the mesothorax (Figs. 1, 4, 12). The metanotum is rigidly fused with the mesopostnotum. The account given for the mesonotum can be directly applied to the metathorax; differences are discussed below.

Panorpidae, Panorpodidae, and Choristidae possess a pair of lateral furrows which arise on the anterior end of the metascutum. These have been termed parapsidal furrows by Issiki (1933), with some reservation. Whether they are would ordinarily have been a minor point, but a condition in Bittacidae complicates the interpretation. There is the additional basic problem as to what exactly are the parapsidal furrows, lines or sutures. There is no general agreement on the use of this term and, when it is encountered, extreme reservation should be exercised in attempting homologies. Those familes which have "parapsidal furrows" have a corresponding internal, anteriorly directed apodeme which arches down to and is fused with the preceding phragma. The structural support provided here is obvious, especially for a relatively weak and highly flexible cuticle as is found in winged Mecoptera. There is no evidence of parapsidal furrows in the other families.

The Bittacidae possess a quadrangular anteromedial plate (Fig. 12, sct) on the metascutum which Setty (1940) termed the prescutum. Whereas this designation may be correct, unequivocable evidence is not available to support it. There are at least two possible explanations for this plate. First, it may indeed be the prescutum; however, by definition (Snodgrass, 1935), the prescutum is that area between antecostal and prescutal sutures. In Bittacidae there is a single anterior transverse suture that by its connection with the phragma is the definitive antecostal suture. The only other suture-like lines are those longitudinal ones on either side of the plate. These lines could have been regarded as the parapsidal furrows, such as are found in some other families; however, they continue mesad posteriorly so that they become a single U-shaped line. This condition could represent fused parapsidal furrows (a condition otherwise unknown in insects) or the prescutal suture (which would be unique to Bittacidae among the Mecoptera), a condition approximated by the adephagous Coleoptera (Snodgrass, 1908). Neither conclusion is entirely satisfactory.

The metapostnotum is fused with a part of tergum 1 of the abdomen, but the separation of the two is indicated by the antecostal suture.

In Boreidae, the metanotum is essentially like the mesonotum except that the metapostnotum is almost twice the size of the mesopostnotum. The condition of the metanotum in Apteropanorpidae is the same as that described for the mesonotum. The metanotum in the apterous and brachypterous Bittacidae conforms with the mesonotal pattern described for these genera. The relative sizes of mesonotum and metanotum vary from one family to another.

PTEROTHORAX: PLEURON

The sternopleural region of insects has long been a subject of controversy and remains so today. The details of this controversy and the major problems which remain to be solved were recently documented by Matsuda (1963b) and DuPorte (1965). The conclusions of the Ferris-Matsuda position stand in contrast to the earlier interpretations of the traditional views advanced by Weber (1928) and Snodgrass (1935). This controversy is particularly germane to a discussion of Mecoptera because some of the arguments of Matsuda (1963b) refer to interpretations of this order and other lower Holometabola. I have accepted the terminology of Matsuda (1960, 1963b) for the pterothoracic pleural region but with reservations on the morphological implications of this stand. This terminology is similar to that of Snodgrass (1927, 1935).

Each pterothoracic pleural field is divided by the vertical pleural suture (ps) into an anterior episternum (eps) and a posterior epimeron (em). The suture extends from the base of the coxa, at the pleural coxal process, dorsally to the base of the wing, where the pleurites taper to form the pleural wing process. Internally the pleural suture is represented by a well developed pleural apodemal process. From approximately the middle of the process the pleural apophysis (pa) extends ventromesally into the thoracic cavity (Figs. 5-6).

The episternum is delimited dorsally from the basalare by the basalar cleft, which in most Mecoptera has become a suture (basalar suture, bs), and ventrally by the coxa. The episternum proper is subdivided into three regions. The dorsalmost anepisternum (aes) is delimited ventrally by the anapleural cleft (ac) or anapleural suture (as, episternal suture of authors). The extent of this suture varies, but it does not reach the pleural suture (except in Nannochoristidae). Immediately below the anepisternum is the preepisternum (pes), which is delimited ventrally by the precoxal suture (pcs, Figs. 19-24). This region has been termed the precoxal bridge (Issiki, 1933). Ventral to the preepisternum is the katepisternum (ks) which is delimited dorsally by the precoxal suture and ventrally by the coxa. The precoxal suture is incomplete and does not reach the pleural suture in most Mecoptera. Generally the extent of the anapleural cleft of the metathorax exceeds that of the mesothorax. In Notiothaumidae (Fig. 24), the precoxal suture of the metathorax is incomplete but attains the pleural suture, while it does not in the mesothorax. The epimeron is usually a single elongate sclerite of simple construction. Situated above the epimeron and surrounded by membrane is the subalare (sb).

The above description is of the mesopleural field but applies also to the metathorax generally. This description holds for the majority of Mecoptera: Panorpidae, Panorpodidae, Choristidae, Nannochoristidae, and Notiothaumidae (Figs. 19-24). The major trend toward reduction of the supracoxal sutures is considered as derived from and representing modifications of the more generalized state seen in Meropeidae, which was elucidated by Matsuda (1960, 1963b) and Mickoleit (1967). The Meropeidae very closely approximate Matsuda's hypothetical pterothoracic segment in which the anapleural ring is completely separated from the ventral katapleural ring by the precoxal suture. The Meropeidae are the only Mecoptera retaining a complete precoxal suture, such as is found in Paleoptera and Neuroptera (Matsuda, 1963b). As a consequence the epimeron of Meropeidae is subdivided into anepimeron and katepimeron.

The Bittacidae are intermediate between most of the families and Meropeidae with respect to pleural development. In Bittacidae the anepisternum is deeply incised by the anapleural suture and the basalare is completely fused with the anepisternum (Fig. 20).

Peculiarities associated with wing reduction are evident in Boreidae and Apteropanorpidae. As Fuller (1954) indicated, the pterothorax of Boreidae is peculiar in that the mesepimeron is fused with the metepisternum so that the pterothoracic pleuron is essentially a single sclerite. Boreidae also lack an anapleural cleft (suture) and a precoxal suture; consequently there is only an episternum separated from an epimeron by the pleural suture (the meron is also greatly reduced). In Apteropanorpidae there is a total fusion of all three thoracic segments with essentially no differentiation in the pterothorax (discussed under the section on the pterothoracic terga).

PTEROTHORAX: STERNUM

Interpretation of the sternal region of Mecoptera encounters the same difficulties as those of the pleural region inasmuch as it has not been resolved for insects in general. However, Weber's study (1928) of the pleurosternal region of Lepidoptera and subsequent studies of other Holometabola by Ferris and Matsuda corroborate the conclusion that in the majority of the Holometabola the sternal field has become invaginated within the thoracic cavity and that in some orders, including Mecoptera, there is no external sternum. The concept of cryptosterny as advanced by Weber (1928, 1933) holds that all of the primary sternal elements and the ventropleurite are invaginated and reduced to a single median longitudinal ridge. Thus, the tendency towards sternal reduction, amalgamation, and invagination seen in the prothoracic sternum reaches its extreme in the pterothorax. The externally visible sclerotized area of the ventral field in the pterothorax of Mecoptera is composed solely of pleural elements.

In the ventral field the preepisternum and katepisternum have shifted anteromesally and terminate at the bases of the coxae (Fig. 8). This is true of the fully winged as well as for the flightless and wingless forms of Mecoptera. The trochantin is retained as a very slender sclerite in the katepisternal area but does not articulate with the coxa or pleuron and has no muscles. The preepisternal and katepisternal elements (Figs. 7-9, 19-24) which occupy the anteroventral field of the pterothoracic segments have collectively been termed by mecopterists the precoxal bridge, a term which has no classical meaning or usage (DuPorte, 1965) but which does have useful descriptive connotations. In his excellent study of the Panorpidae and Panorpodidae, Issiki (1933) regarded the ventral field anterior to the coxae as a combination of the precoxal bridge and the basisternite, that posterior to the coxae as furcasternite, the ventralmost part of which forms an articulation with the mesal side of the coxa. This interpretation is based on external studies, and as a consequence Issiki was not able to observe the well developed internal structure of the cryptosternite (Figs. 3a-g, 10-11, 13). There are also some inconsistencies in the terminology of Ferris and Rees (1939) but the synonomies have been worked out by Matsuda (1960, 1963b).

Internally the pleurosternal region is a complex of apodemes and apophyses which vary depending upon the flight function. In some instances the axial orientation depends upon whether the organism is compressed (the majority of Mecoptera) or depressed (Meropeidae and, to a lesser extent, Notiothaumidae).

In the majority of Mecoptera (Panorpidae, Panorpodidae, Choristidae, Nannochoristidae, Notiothaumidae, Bittacidae and Meropeidae) the pleurosternal region consists of the following elements. The episternum has an anterior apodeme which begins just below the anapleural cleft and extends ventrally to the level of the coxa where it turns mesad and becomes continuous with the sternal apodeme (Fig. 5). There is also a ventral apophysis of the pleural apodeme at the base of the coxa which extends slightly into the coxal cavity. At the anterior edge of the sternum there is a dorsally projecting apophysis. On the posterior edge of the epimeron there is a dorsoventral apodeme delimited dorsally by the lateropostnotum and terminating ventrally at the base of the epimeron. The furca is highly developed in Mecoptera and bears an anterior tendon above its base. Extending ventrally from the median longitudinal ridge on either side is a V-shaped sclerotized area. Anteriorly this area is continuous with the precoxal bridge. Ventrally it terminates in an articulation with the coxa. It is dorsoventrally divided by a suture coming down from the furca (Figs. 3a-g, 5-6, 10-11, 13).

This sclerite has been regarded as the furcasternite (Issiki, 1933), the pleurum (Ferris and Rees, 1939), the sternal ridge (Hasken, 1939), and the sternum (Fuller, 1954; Mickoleit, 1967). The authors after Issiki who have termed this area the sternum or process thereof are in accord with the interpretation of Matsuda (1960, 1963b). To consider the median longitudinal ridge, the furca, and these ventral extensions as the sternum of Mecoptera is the view taken here—and one that is consistent with the Weber-Ferris-Matsuda line of thinking on the sternum of Holometabola and in particular of Mecoptera.

The sternal modifications in the brachypterous forms (Boreidae and *Anomalobittacus*) and apterous forms (Apteropanorpidae and *Apterobittacus*) are minor; that is, they present no special problems of interpretation but are characterized by a reduction in the development of apodemes and apophyses in the sternopleural region. Details in the Boreidae are discussed by Fuller (1954). The sternal structure in Apteropanorpidae is simplified through suppression of the various apodemes and apophyses.

LEGS

Concomitant with the involution of the sterna, the coxae of all thoracic segments have become mesally displaced such that they are somewhat appressed against one another. As Issiki (1933) pointed out, the coxae of Mecoptera are not as freely movable as are those of other orders in which they are widely separated by a well developed sternum. In addition there are some basic differences in the structure of the procoxae and in the pterothoracic coxae of Mecoptera.

The coxa of the prothorax in all families of Mecoptera is a hollow cylinder attached to the thorax by a coxal membrane or conjunctiva (the coxal articular corium). The coxa is laterally tapered at its connection with the trochanter. At its proximal end it forms a typical monocondylic articulation with the pleuro-coxal hinge process of the propleuron. Just below its base, the coxa is circumscribed by a submarginal basicostal suture represented internally by an apodemal ridge, the basicosta. Proximad of the basicostal suture is a thin, flattened flange on either side of the pleuro-coxal articulation, the basicoxite, which is confluent with the coxal shaft toward the mesal plane.

There is no trace of a meron in the prothoracic leg of any Mecoptera, although Hasken (1939) designates the post-articular basal apodeme as the merocosta and the rim basal to it as the merocoxite. These designations are unacceptable because there is no indication of a coxal (or meral) suture in the prothoracic coxa.

The pterothoracic coxae are more complex than those of the prothorax and possess a ventral articulation. They are basically cylindrical or conical and articulate with the respective trochanters by two well developed condyles (Fig. 15). Like the procoxa, the pterocoxa has an exterior pleuro-coxal articulation formed by a process at the ventral end of the pleural suture and a process at the proximal end of the coxa, at the base of the coxal (or meral) suture. On the mesal side the coxa has a condylar articulation with the ventral process (sternal ridge, sr, Figs. 6, 10-11) of the sternum, which is the best developed of the articulations. A third articulation, commonly encountered in other insects (Snodgrass, 1935), is a trochantinal articulation, but in Mecoptera the trochantin is greatly reduced and the articulation non-existent. Issiki (1933) analyzed all three of these articular points in Panorpidae and Panorpodidae and found that all of them are poorly developed in comparison with other insect groups; this is true of the other families of Mecoptera as well.

The pterothoracic coxa is dorsoventrally divided by the coxal suture into an anterior eucoxa and a posterior meron (one of the classical characteristics that define the Panorpoid Complex). In addition, there is the basicostal suture which circumscribes the proximal end of the coxa as in the procoxa. That portion anterior to the coxal suture (which appears as a ventral continuation of the pleural suture) is the basicoxite; below it is the basicostal flange-like apodeme; that posterior to the coxal suture is the corresponding merocoxite and merocosta. Ventrally the meron terminates just above the coxo-trochanteral articulation by the ventrolateral curvature of the coxal suture in the metathorax. At this point (the apex or distal end of the meron) the area above the posterior coxo-trochanteral articulation is greatly reenforced. Snodgrass (1935) states that the meron never includes the region of the posterior articulation and that it is always cut off by the coxal suture. This is not the case in the mesocoxa of most Mecoptera. In all mecopteran families except Boreidae and Apteropanorpidae the tip of the meron of the mesothorax is continuous with the distal end of the coxa and does in fact bear the posterior coxo-trochanteral condyle (Fig. 15). Hasken (1939) recognized this relationship in Panorpidae.

In Boreidae the only evidence of meral development in the pterothorax is a very short coxal suture that barely extends beyond the basicosta, with the result that the meral area is vestigial at the proximal part of the coxa. The Boreidae are unique in that they are the only jumping Mecoptera. The modifications to meet this mode of locomotion are discussed in fine detail by Fuller (1954, 1955). The structure of the coxa in Apteropanorpidae is reminiscent of the generalized prothoracic coxa of the order. There is no trace of a meron, coxal suture, merocosta, or merocoxite. The meron plays no part in the coxo-trochanteral articulation in either pterothoracic leg of Boreidae or Apteropanorpidae.

Internally the basicosta extends mesoventrally to the sternocoxal articulation in the dorsoventral plane; the other coxal process is parallel to the longitudinal axis of the body and terminates at the posteroventral end of the trochantin (though the articulation is functionless). Likewise the coxal (or meral) suture internally gives rise to a meral apodeme that relates to the coxo-trochanteral posterior joint (see above). In all coxae there is a trochanteral tendon to which coxal muscles attach (discussed under musculature). In general, the relative size of the coxae increases from prothorax to metathorax with the notable exception of Nannochoristidae in which the mesothorax and its legs comprise the largest of the thoracic segments.

The legs of Mecoptera consist of the typical number of segments; coxa, trochanter, femur, tibia, tarsus (of five tarsomeres) and pretarsus. The coxa was discussed with the pleurosternal region because of its close affinity with the latter.

The Mecoptera are divisible, on the basis of leg structure, into walking (most Mecoptera), jumping (Boreidae) and raptorial (Bittacidae) insects, each with modifications peculiar to the activity. In a detailed study of Bittacid legs, Röber (1942) analyzed the fine points of their structure and function (Figs. 18a-c). He likewise based some observations on his comparative study of other families. Fuller (1955) analyzed the jumping function in Boreidae. The remaining families have generalized legs with the normal functions (Snodgrass, 1935).

The trochanter (tr) is a short, slightly compressed, curved segment in Mecoptera. It has a dicondylic articulation with the coxa. At its distal end it has an outer and an inner syndetic articulation at the trochantero-femoral joint, which allows only a very slight horizontal oscillation of the femur on the trochanter. The trochanter has a proximal tendon on which the coxal muscles insert. At the distal end there is a tendon for the attachment of trochanteral muscles.

The femur (Fig. 14) is the largest leg segment. The femoro-tibial joint is a dicondylic articulation of the anterior-posterior type.

The tibia (Fig. 14) is slightly curved at its proximal end and internally bears a dorsal extensor tendon and a ventral flexor tendon for the tibial extensor and flexor muscles, respectively. In the Bittacidae there are inner and an outer tibial extensor tendons, and the muscles are also divided (Fig. 16). On the distal inner side of the tibia is a pair of articulated tibial spurs.

The tarsus is composed of five tarsomeres, the basal of which bears both the tarsal flexor and extensor tendons at its proximal end.

The pretarsus (pt) is essentially the same in all Mecoptera except the Bittacidae (Figs. 17, 18a-c). The general account of the pretarsus which Issiki (1933) gives of Panorpidae suffices for the majority of families. The pretarsus arises from the apex of the last tarsomere to which it is connected by a membrane. Dorsolaterally there is a pair of tarsal claws (ungues), with an arolium (ar) between them. The arolium is a pad-like continuation of the median pretarsal base. It is mostly membranous but has sclerotized rods of variable dimensions. Basally it is supported by an auxilliary plate (Hilfsplatte of German authors). Dorsally the unguifer articulates with the claws, is internally produced and not externally visible. The unguitractor plate is partially invaginated within the distal tarsomere on the ventral side of the pretarsus. Distal to the unguitractor is a small sclerite, the planta (pl). At the base of each claw and extending ventrolaterally on each side is a slender sclerite, the auxillia (ax). From the unguitractor plate the long pretarsal tendon, to which the tibial and femoral pretarsal effector muscles attach, extends through the tarsomeres and tibia and into the femur.

This adequately describes the structure of the pretarsus in the majority of families. There are a few exceptions, such as the absence of an arolium in Notiothaumidae and Boreidae and the fact that the unguitractor plate is deeply invaginated within the apical tarsomere in Notiothaumidae and Panorpodidae. The Bittacidae constitute the single major exception in which all of the pretarsal elements have become amalgamated into a single heavily sclerotized claw associated with the raptorial function of the leg in this family (Figs. 18a-c; Röber, 1942).

SPIRACLES

It is characteristic of the Pterygota that all of the postembryonic stages have but two pairs of thoracic spiracles. Primitively, the first belongs to the mesothorax and the second to the metathorax (Snodgrass, 1935). However, there is a tendency for the spiracles to become secondarily displaced anterodorsally so that they occupy an intersegmental position—the first between the prothorax and mesothorax and the second between the mesothorax and metathorax—as is the case in most Mecoptera.

It is characteristic of Mecoptera that the thoracic spiracles are considerably larger than those of the abdomen and that the muscular effectors in the two tagmata differ (Hassan, 1944). With the exception of Boreidae and Apteropanorpidae, the thoracic spiracles of Mecoptera are obliquely oriented in the intersegmental area above the anapleural cleft (or suture). Each spiracle consists of two elongate lips that appress one another in the closed position and which open into an atrium from which tracheae ramify.

Exceptions to this arrangement occur in the Bittacidae, in which the metathoracic spiracle has a single external lid, and in the Boreidae and Apteropanorpidae, in which the mesothoracic spiracle has become secondarily displaced into the posterolateral part of the pronotum and the metathoracic spiracle lies in the fused mesepimeron-metepisternal area. The thoracic spiracles of these last two families are devoid of external lids or covering of any kind. A comparative account of the spiracles of Mecoptera and their allies is given by Hassan (1944).

In those families which have a two-lipped closing apparatus, there is an occlusor muscle which extends from the ventral end of the spiracle on an apodeme to the anterior apodeme below and behind it. The first spiracular muscle terminates on the anterior apodeme of the mesepisternum (Figs. 25-26), the second on the anterior apodeme of the metepisternum. The closing mechanism and structure are described by Hassan (1944). The thoracic spiracles are conspicuously larger than those of the abdomen and differ from the latter in having a single occlusor muscle, while there are two occlusor muscles for each abdominal spiracle. Those families which lack the normal external lids and in which the spiracles are firmly imbedded in the nota (Boreidae and Apteropanorpidae) also lack spiracular occlusor muscles.

PTEROTHORAX: Musculature

The pterothoracic musculature presents several interesting problems. The first concerns the differences between the prothoracic musculature and that of the pterothorax. Although all three of the thoracic segments have a homodynamous relationship, their skeletal and muscular elements are quite different. These muscles were initially recorded by Hasken (1939). The problem of homologizing the muscles of mesothorax and metathorax is lesser and was also resolved by Hasken. Perhaps the most difficult problem in the study of the pterothoracic muscles of Mecoptera is resolving modifications (including those of the skeleton) as they relate to the flight function, since the order includes apterous and brachypterous species as well as the majority of normal fliers.

As Maki (1938) pointed out, the degree of difference between mesothoracic and metathoracic musculature varies in different orders; but these differences are slight in Mecoptera. There is also a close correspondence of these muscles within the Panorpoid Complex as compared to other Holometabola (Maki, 1938).

The following account of the pterothoracic musculature is based on the mesothorax. The close agreement of the metathoracic muscles with those of the mesothorax obviates the need for a separate description. For purposes of comparison, only the fully winged Bittacidae are used along with the other families; that is, there is no special consideration of reduction or loss in such genera as *Apterobittacus* and *Anomalobittacus*. The Apteropanorpidae are treated as the apterous group and the Boreidae as the brachypterous group. The musculature of the nine families is tabulated in Tables 3 and 4.

Intersegmental Muscles

LONGITUDINAL MUSCLES (Figs. 25-26)

dlm$_1$. Between phragmata 1 and 2. It completely covers phragma 1 and part of the scutum on the anterior end and on the posterior end covers phragma and part of the postnotum. It is cuneiform in cross-section and is an indirect depressor of the wings.

dlm$_2$. Lateral edge of phragma 2 on the lateropostnotum to the side of the scutum. It is an indirect flight muscle which in conjunction with dvm muscles functions as a levator of the wing. As such, it is antagonistic to dlm$_1$ and also depresses the scutum.

dlm$_3$. This is a very small muscle from the scutoscutellar apodeme to the anterior side of the postnotum.

vlm. Base of the posterior side of the mesofurca to the middle of the anterior side of the metafurca where it ends in a short tendon.

Segmental Muscles

DORSOVENTRAL MUSCLES (Figs. 25-26)

dvm$_1$. Lateral part of the scutum ventrally to the anterior side of the sternal apophysis on the preepisternum.

dvm$_2$. Immediately behind dvm$_1$ on the scutum ventrally to the trochantin. This is the only muscle of the trochantin.

dvm$_3$. Lateral part of the scutum anterior of the scutellum and behind dvm$_2$ to the long trochanteral tendon; a tergal depressor and femoral abductor. It is especially well developed in Boreidae (Fuller, 1955).

dvm$_4$. Scutum behind dvm$_3$ and ventrally at an oblique angle to the posterior side of the meron. The dorsoventral muscles collectively depress the tergum through their action on the scutum and are indirect flight muscles in conjunction with the dorsal longitudinal muscles (dlm_2). In addition, dvm_2 and dvm_4 impart a slight amount of flexion to the coxa.

TRANSVERSE MUSCLES (Figs. 25-26)

zm. Apex of the furcal arm to the pleural apophysis.

ifum. Between the arms of the furca. It is antagonistic to the sternal leg muscles and draws the furcal arms towards the midline.

PLEURAL MUSCLES (Figs. 27-28)

pm_1. Precoxal bridge to the inner dorsal side of the episternal tendon; an alary abductor.

pm_2. Outer edge of the basicosta dorsally to the anepisternal tendon and to the tendon above the anapleural cleft; elevates the wing.

pm_3. Inner edge of the trochanteral tendon to the dorsal anepisternal tendon; an alary abductor and femoral adductor.

pm_4. Merocosta just behind the pleuro-coxal articulation to the subalare; an alary adductor.

pm_5. Pleural apodeme to the first axillary sclerite; an alary rotator.

pm_6. Immediately behind pm_5 and to the side of the scutum; an alary rotator.

pm_7. Pleural apodeme immediately behind pm_6 to the posterior hinge process. All three of these rotators, pm_{5-7}, arise on short tendons one behind the other and effect rotation of the wing. The muscle pm_6 is also a flexor of the tergum (Hasken, 1939). Occasionally, as in Boreidae (Fuller, 1955), there is a single alary rotator instead of three.

pm_8. Anepisternal hinge process to the tegula; a protractor of the wing.

pm_9. Anapleural cleft to a tendon of the third axillary sclerite; a retractor of the wing.

pm_{10}. Below the end of the episternum to the lateral edge of the basicosta in a tendon near pm_2; a promotor of the coxa.

pm_{11}. Dorsal side of a tendon process on the base of phragma I anteriorly to the side of the scutum; an accessory of the large dorsal longitudinal muscle dlm_1.

pm_{12}. Dorsal end of the posterior epimeral apodeme to a tendon cap of the subalare.

pm_{13}. Anterior episternal apodeme dorsally across the anapleural cleft to the anepisternal side of the cleft; when the cleft is membranous as opposed to sutured, the muscle closes the cleft.

pm_{14}. Below pm_{13} on the anterior apodeme dorsally to the tendon process on the side of pm_{13}; effects closure of the anapleural cleft.

pm_{15}. Just above pm_{13} and pm_{14} to the lateral edge of the scutum; it functions antagonistically to pm_{13+14}.

pm_{16}. Pleural apodeme to a dorsal process of the subalare.

pm_{17}. Ventral end of the pleural apodeme to the subalare in a tendon next to pm_4 to which it is an accessory; an alary adductor.

During the course of this study it was not possible to dissect any specimens of Choristidae; consequently, only conjectures were available as to the probable musculature of the members of this family. Shortly after the completion of this work, Mickoleit (1969) published a report on the pterothoracic pleurosternal musculature of Panorpidea and Neuropteroidea. His findings for *Taeniochorista* (Choristidae) confirm the supposition that the pleurosternal muscles ("pm" series) are indeed present in the same number and arrangement as suggested in this paper. The findings of Storch and Chadwick (1968) for Bittacidae agree with my own findings in this family.

Leg Muscles

STERNAL MUSCLES (Figs. 25-26)

bm_1. Anterior side of the mesofurca to a terminal apophysis of the pleural apodeme at its ventral end; antagonistic to cxm_1.

bm_2. Membranous area on the inner side of the sternal apodeme near the base of the furca to the medial side of the trochanteral tendon on the middle of its base, laterad of dvm_3; a femoral abductor.

bm_3. Sternal apodeme to the posterior side of the basicosta; a coxal promotor. This muscle is regarded as subdivided (Hasken, 1939). The second band is parallel to the first and has the same origins and insertions as the former.

bm_4. Base of the posterior side of the sternal apodeme to a tendon on the distal end of the meron.

bm_5. The first band from the posterior side of the sternal apophysis to the posterior side of the basicosta; the second from the posterior side of the sternal apophysis to the medial side of the meron; a coxal remotor. This muscle is also considered as divided (Hasken, 1939).

COXAL MUSCLES (Figs. 25-27)

cxm_1. Anterior surface of the eucoxa to the trochanteral tendon in front of cxm_2.

cxm_2. Basicosta (sometimes part of the origin is on the merocosta) to the proximal end of the trochanteral tendon.

cxm_3. Ventral process of the pleural apodeme to the lateral proximal end of the trochanteral tendon; *cxm_{1-3}* are femoral adductors.

cxm_4. Anteromedial side of the coxa to the base of the trochanteral tendon on the ventral side.

cxm_5. Anterior side of the coxa between cxm_1 and cxm_4 to the trochanteral tendon.

TABLE 3. Mesothoracic Musculature.

	CHORISTIDAE	NANNOCHORISTIDAE	BITTACIDAE	PANORPODIDAE	PANORPIDAE	BOREIDAE	MEROPEIDAE	NOTIOTHAUMIDAE	APTEROPANORPIDAE
dlm_1	+?	+	+	+	+	—	+	+	—
dlm_2	+?	+	+	+	+	—	+	+	—
dlm_3	+?	—	—	+	+	—	—	—	—
vlm	+?	+	+	+	+	—	—	+	+
dvm_1	+?	+	+	+	+	—	+	+	—
dvm_2	+?	+	+	+	+	—	+	+	—
dvm_3	+?	+	+	+	+	+	+	+	—
dvm_4	+?	+	+	+	+	—	+	+	—
zm	+?	+	+	+	+	—	+	+	+
pm_1	+?	+	+	+	+	—	+	+	+
pm_2	+?	+	+	+	+	+	+	+	+
pm_3	+?	+	+	+	+	—	+	+	+
pm_4	+?	+	+	+	+	+	+	+	—
pm_5	+?	+	+	+	+		+	+	—
pm_6	+	+	—	+	+	+	+	+	—
pm_7	+	+	+	+	+		+	+	—
pm_8	+	+	+	+	+	—	+	+	—
pm_9	+	+	+	+	+	—	+	+	—
pm_{10}	+?	+	—	+	+	+	+	+	—
pm_{11}	+	+	+	+	+	—	+	+	—
pm_{12}	+?	+	+	+	+	—	+	+	—
pm_{13}	+?	+	+	+	+	—	+	+	—
pm_{14}	+?	+	+	+	+	—	+	+	—
pm_{15}	+	+	—	+	+	—	+	+	—
pm_{16}	+?	+?	+	+	+	—	+	+	—
pm_{17}	—?	—	—	—	—	+	—	—	—
bm_1	+?	+	+	+	+	+	+	+	+
bm_2	+?	+	+	+	+	+	+	+	+
bm_3	+?	+	+	+	+	+	+	+	+
bm_4	+?	+	+	+?	+	+	+	+	+
bm_5	+?	+	+	+	+	+	+	+	+
cxm_1	+?	+	+	+	+	+	+	+	+
cxm_2	+?	+	+	+	+	+	+	+	+
cxm_3	+?	+	+	+	+	+	+	+	+
cxm_4	+?	+	+	+	+	+	+	+	+
cxm_5	+?	+	+	+	+	+	+	+	+
cxm_6	+?	+	+	+	+	+	+	+	+
cxm_7	+?	+	+	+	+	+	+	+	+
mrf	+?	+	+	+	+	+	+	+	+
mft	+?	+	+	+	+	+	+	+	+
met	+?	+	+	+	+	+	+	+	+
mfp_1	+?	+	+	+	+	+	+	+	+
mfp_2	+?	+	+	+	+	+	+	+	+
mfa	+?	+	+	+	+	+	+	+	+
mea	+?	+	+	+	+	+	+	+	+
ifum	+?	+	—	+	+	—	—	—	—?
om	+?	+?	+	+	+	+	+	+	—

TABLE 4. Metathoracic Musculature.

	CHORISTIDAE	NANNOCHORISTIDAE	BITTACIDAE	PANORPODIDAE	PANORPIDAE	BOREIDAE	MEROPEIDAE	NOTIOTHAUMIDAE	APTEROPANORPIDAE
dlm$_1$	+ ?	+	+	+	+	—	+	+	—
dlm$_2$	+ ?	+	+	+	+	+	+	+	—
dlm$_3$	— ?	—	—	—	—	—	—	—	—
vlm	+ ?	+	+	—	+	+	+	—	—
dvm$_1$	+ ?	+	+	+	+	—	+	+	—
dvm$_2$	+ ?	+	+	+	+	—	+	+	—
dvm$_3$	+ ?	+	+	+	+	+	+	+	—
dvm$_4$	+ ?	+	+	+	+	—	+	+	—
zm	+ ?	+	+	+	+	—	+	+	+
pm$_1$	+ ?	+	+	+	+	—	+	+	+
pm$_2$	+ ?	+	+	+	+	+	+	+	+
pm$_3$	+ ?	+	+	+	+	—	+	+	—
pm$_4$	+ ?	+	+	+	+	+	+	+	—
pm$_5$	+ ?		+	+	+		+	+	—
pm$_6$	+	+	+	+	+	+	+	+	—
pm$_7$	+		+	—	—		+	+	—
pm$_8$	+	+ ?	+	+	+	—	+	+	—
pm$_9$	+	+ ?	+	+	+	—	+	+	—
pm$_{10}$	+ ?	+ ?	—	+	+	+	+	—	—
pm$_{11}$	+	+ ?	+	+	+	—	+	+	—
pm$_{12}$	+ ?	+ ?	+	+	+	—	—	—	—
pm$_{13}$	+ ?	+ ?	+	+*	+	—	+	+	—
pm$_{14}$	+ ?	+ ?	+	+*	+	—	+	+	—
pm$_{15}$	+	+ ?	+	+	+	—	+	+	—
pm$_{16}$	+ ?	+ ?	+	+	+	—	+	+	—
pm$_{17}$	— ?	— ?	—	—	—	—	—	—	—
bm$_1$	+ ?	+	+	+	+	+	+	+	+
bm$_2$	+ ?	+	+	+	+	+	+	+	+
bm$_3$	+ ?	+	+	+	+	+	+	+	+
bm$_4$	+ ?	+	+	+ ?	+	+	+	+	+
bm$_5$	+ ?	+	+	+	+	+	+	+	+
cxm$_1$	+ ?	+	+	+	+	+	+	+	+
cxm$_2$	+ ?	+	+	+	+	+	+	+	+
cxm$_3$	+ ?	+	+	+	+	+	+	+	+
cxm$_4$	+ ?	+	+	+	+	+	+	+	+
cxm$_5$	+ ?	+	+	+	+	+	+	+	+
cxm$_6$	+ ?	+	+	+	+	+	+	+	+
cxm$_7$	+ ?	+	+	+	+	+	+	+	+
mrf	+ ?	+	+	+	+	+	+	+	+
mft	+ ?	+	+	+	+	+	+	+	+
met	+ ?	+	+	+	+	+	+	+	+
mfp$_1$	+ ?	+	+	+	+	+	+	+	+
mfp$_2$	+ ?	+	+	+	+	+	+	+	+
mta	+ ?	+	+	+	+	+	+	+	+
mea	+ ?	+	+	+	+	+	+	+	+
ifum	— ?	—	—	—	—	—	—	—	—
om	+ ?	+ ?	+	+	+	+	+	+	—

* pm$_{13}$ and pm$_{14}$ fused

cxm_6. Posterior side of the coxa to the posterior side of the trochanteral tendon; antagonitic to cxm_5; cxm_{4-6} are femoral rotators.

cxm_7. Posterior side of the basicosta to the proximal edge of the trochanter behind cxm_2; an accessory femoral adductor to cxm_{1-3}.

TROCHANTERAL MUSCLES (Fig. 14)

mrf. Proximal part of the trochanter to a tendon that originates on the anterolateral side of the femur; a femoral rotator. This is a large muscle which completely occupies the trochanter.

FEMORAL MUSCLES (Figs. 14, 16)

mft. Trochanter to the tibial tendon; works in conjunction with the next muscle; tibial flexor.

mft. Ventral wall of the femur to a corresponding position on the base of the large tibial tendon which occupy most of the rest of the femur; tibial flexor.

met. Lies opposite the inferior flexor dorsally from its origin to the corresponding position on the dorsal proximal end of the tibia; a tibial extensor.

mfp_1. Proximal end of the femur to the long pretarsal tendon which passes through the femur, tibia and tarsus and terminates on the pretarsal unguitractor plate; a pretarsal flexor.

TIBIAL MUSCLES (Fig. 14)

mfp_2. Proximal end of the tibia to the pretarsal tendon; an accessory of the superior pretarsal flexor.

mfa. Ventral distal end of the tibia to the proximal end of the first tarsomere; a tarsal flexor.

mea. Lies opposite the tarsal flexor and has the corresponding origin and insertion points; dorsal to the flexor and antagonistic to it; a tarsal extensor.

DISCUSSION AND CONCLUSIONS

The cervix of Mecoptera is well developed and has a pair of laterocervicalia and in some families a pair of dorsocervicalia. It is suggested that the dorsocervicalia arose by fragmentation from the postocciput and that their function as points of muscle insertion is derived.

The dorsal longitudinal muscles of the cervix ($Odlm_{1-2}$) have no direct relationship to the prothorax in terms of origins and insertions, since in generalized insects they extend from phragma 1 to the head capsule (Snodgrass, 1935). The occurrence of $Odlm_2$ in Boreidae and Notiothaumidae is probably secondarily derived. The ventral longitudinal muscles ($Ovlm_{1-2}$) are also considered to be derived by fragmentation from a single band (Hasken, 1939).

The oblique intersegmental muscles ($Oism_{1-5}$) are variable; reduction in this series occurs in those families in which there is a general trend toward reduction of the entire cervical field (Boreidae, Bittacidae, and Meropeidae). Only the Notiothaumidae possess the full complement of cervical muscles with secondary subdivisions (i.e., with $Oism_4$ subdivided into two bands).

The pronotum of Mecoptera is variously creased with transverse furrows whose inner surfaces form apodemes for muscle attachments. The pleural region tends toward reduction and fusion into a single complex involving the proepimeron, proepisternum, profurca, and the pleural apodeme. A trochantin is present but does not articulate with the coxa nor have any muscles attached to it, an arrangement seen also in the higher Pterygota. The prosternum is reduced, compared with that of generalized insects. The sternal elements are fused into a plate containing the eusternum, furcacavae, and spinasternum. The entire sternal complex is involuted and there is no trace of a sternacostal suture.

Although there is considerable variation in the prothoracic pleural region and in the extent of the pronotum, the number of prothoracic muscles is rather constant for the order. Nothing of the trends in the evolution of these muscles is evident within Mecoptera, but when Mecoptera are compared with other orders of the Panorpoid Complex the following patterns emerge.

The intersegmental prothoracic dorsal longitudinal muscles (ldlm) of Mecoptera are disconcerting because they occur only as median dorsal muscles, while in other Panorpoid orders there are lateral and anterior dorsals as well. Three possible sets of these muscles are present in the lower orders (Maki, 1938), and it is presumed that the described reduction is restricted to Mecoptera. The prothoracic ventrals offer nothing noteworthy.

Of the prothoracic segmental muscles, the dorsoventral and pleural muscles are constant within Mecoptera and in the other orders of the Panorpoid Complex. The intrafurcal muscle (1ifum) occurs only in Mecoptera and tipulid Diptera (Maki, 1938). The dorsoventral muscles are also constant within Mecoptera and the Panorpoid orders, but the overall trend is toward reduction in the number of these muscles in the Panorpoid Complex as compared with Neuroptera. There is also a reduction and loss of anterior external dorsoventral muscles from the entire Panorpoid Complex, while these muscles are retained in Neuroptera (Maki, 1938; Kelsey, 1957).

The pleural prothoracic muscles are uniformly present in Mecoptera but vary within the Panorpoid Complex and in the lower orders. There is no clear pattern to their presence or absence within the Complex. Sternopleural muscles are absent from the prothorax of Mecoptera and from most of the Panorpoid orders. There is a reduction in the total number of procoxal muscles (cxm series) within Mecoptera and allies as compared with the lower orders.

The pterothoracic notum of Mecoptera is of the generalized type. Modifications which do occur include a fusion of the notal sclerites into a single plate in brachypterous and apterous species. It is remarkable that the alinotum and postnotum of Mecoptera are separated by a secondary intrasegmental conjunctiva since this conjunctiva is lost in higher Pterygota. An extreme is reached in Apteropanorpidae in the complete fusion of the notal and pleural sclerites into a single plate.

The pterothoracic pleuron of Mecoptera is well developed and contains most of the sclerites of the hypothetical type (Matsuda, 1963b). This is especially true of Meropeidae and Notiothaumidae (sometimes placed together in a separate suborder, Protomecoptera, from the other families of Mecoptera). In other Mecoptera the trend is toward a loss of the coxopleural elements posterior to the pleural suture. This is considered to be a derived state, resembling the situation in higher Pterygota. Modifications associated with wing reduction, in Boreidae and Apteropanorpidae, include fusion of the pleurites.

The tendency toward involution of the sternum, seen in the prothorax, reaches an extreme in the pterothorax. There are no sternal elements externally visible in the pterothorax. The view taken here follows the Weber-Ferris-Matsuda line of thought, namely, that the pterothoracic sternum of Mecoptera and of other Panorpoid orders consists only of the internal median longitudinal ridge, the furca, and the sternal ridge of the sterno-coxal articulation.

The articulations of the coxae with the thorax are restricted and reduced compared with those of other higher Pterygota. The normal trochantino-coxal articulation found in other insects (Snodgrass, 1935) is absent from Mecoptera. The coxa is dorsoventrally subdivided into a eucoxa and a large meron. In addition, it is laterally circumscribed by the basicostal suture which sets off a small basicoxite and merocoxite. The mesocoxa of Mecoptera is unusual in that the posterior articulation of the coxa with the trochanter directly involves the meron.

The peculiarities and limitations of leg movement in Mecoptera are largely due to alterations in articulations and not to loss of muscles, since there are sufficient promotor and remotor muscles to allow versatile movement. The prothoracic leg muscles are essentially the same as those of the pterothorax. In the other Panorpoid orders there is a tendency toward modification and loss of some of these muscles (Maki, 1938).

The intersegmental pterothoracic longitudinal muscles (dlm$_{1-2}$) of Mecoptera are present in all of the normally winged species, with loss occurring in the apterous species. This pattern varies slightly in other orders of the Panorpoid Complex. An unusual, very small muscle (dlm$_3$) is found in the mesothorax of Panorpidae and Panorpodidae. The ventral longitudinals (vlm) are more variable within the order but are generally present, although they do not exhibit any clear pattern.

The dorsoventral segmental muscles are essentially the same for both pterothoracic segments but are absent from apterous Mecoptera. These muscles correspond with those of other orders of the Panorpoid Complex and collectively show a reduction in number from those of lower Pterygota. There is nothing unique about the furcal muscle (zm) in Mecoptera or related orders, but it is curious that it is absent from the brachypterous Boreidae but present in the apterous Apteropanorpidae, in both pterothoracic segments.

The complex set of pleural muscles is the most variable in the pterothorax of Mecoptera and other Panorpoid orders, a fact easily anticipated in view of the modifications of the pterothorax related to flight. Maki (1938) pointed out that there is a greater uniformity in the meso- and metathorax of neuroptera than in any of the other higher Pterygota. In Mecoptera, as well, there is a very close correspondence in these muscles between the segments within a family but more variation between families. Those muscles related to flight are naturally present in the flying forms but are totally lost as aptery is approached. Variation in the occurrence of these muscles among fully winged species must relate in some manner to peculiarities of flight within the order, but to establish this would require a detailed comparative study of flight dynamics.

The series of pleural muscles (pm_{1-4}) present in the pterothoraces of all fully winged Mecoptera tend to reduction with aptery. The series pm_{5-7} varies within the order and comprises very small alary rotators. There is a tendency to reduction in the number of these muscles within the metathorax, but it is difficult to determine exactly which ones of the series remained and which were lost. The muscles pm_{8-9} lie in the same plane as pm_{5-7} and are present in all of the fully winged species but are absent from Boreidae and Apteropanorpidae. The muscle pm_{10} is peculiar in that it is constant among all winged families (except Bittacidae) but is absent from the brachypterous and apterous species and from the metathorax of Notiothaumidae. There is nothing noteworthy about the series pm_{11-12}, pm_{13-15}, and pm_{16}. The muscle pm_{17}, unique to the mesothorax of Boreidae, does not represent a special case or a new muscle but an unidentified one of the pleural series not homologized by Fuller (1955).

The major trend in the evolution of the pterothoracic musculature involves a reduction in the total number of muscles, as compared to the thoracic musculature of the lower Pterygota. In the existing muscles, there is a trend toward secondary splitting.

This study has shown that there is a definite, basic anatomical pattern in the order Mecoptera, that is, one to which all of the families in general correspond. Naturally, some families fit the generalized condition more precisely than others do. Skeletal and muscular structures of the head and thorax suggest certain conclusions to the relative closeness of one family to another and the position of the order with respect to other insect orders.

Meropeidae is judged the most primitive family within the order since it shows the greatest concentration of primitive or generalized features, particularly in the thoracic skeleton and musculature. Notiothaumidae, while not as generalized as Meropeidae, retains a greater number of these primitive characters than do the other families and hence appears to have the greatest taxonomic affinity to Meropeidae. I think that these two families are aptly placed in the suborder Protomecoptera.

The families Panorpidae, Panorpodidae, Choristidae, and Nannochoristidae share a more advanced state of organization than is seen in the Protomecoptra. These four families represent an intermediate stage in the graduation of anatomical features within Mecoptera. Boreidae, in my estimation, also belongs with these intermediate families, in spite of its many thoracic modifications. In this connection, I think that attempts to remove the Boreidae (Hinton, 1958) to a separate order Neomecoptera are unjustifiable.

Bittacidae are structurally the most advanced family of Mecoptera. This family is a good example of the transition from a morphologically primitive state, as in Meropeidae, to that of the higher holometabolous orders. The family Apteropanorpidae remains enigmatic because of the extreme reduction in its thoracic development. I am inclined to think that this family represents an extreme modification of the intermediate level of organization.

In terms of classification, these findings (which are based on an entirely different set of anatomical structures) in general support the recently proposed classification of Byers (1965), although he regarded the Choristidae as the most generalized family. I think the soundness of that classification is demonstrated by the fact that, in the course of this study, an anatomical "family pattern" was found which corresponded in each case to the familial taxa recognized by Byers.

The order Mecoptera as a whole has emerged at the base of the Panorpoid Complex and is structurally more primitive or generalized than any of the sister orders within the Complex. Accordingly, Mecoptera retain a level of organization at the base of the Holometabola, alongside the Neuroptera, just as Tillyard (1918a & b, 1919, 1935) suggested in his study of half a century ago.

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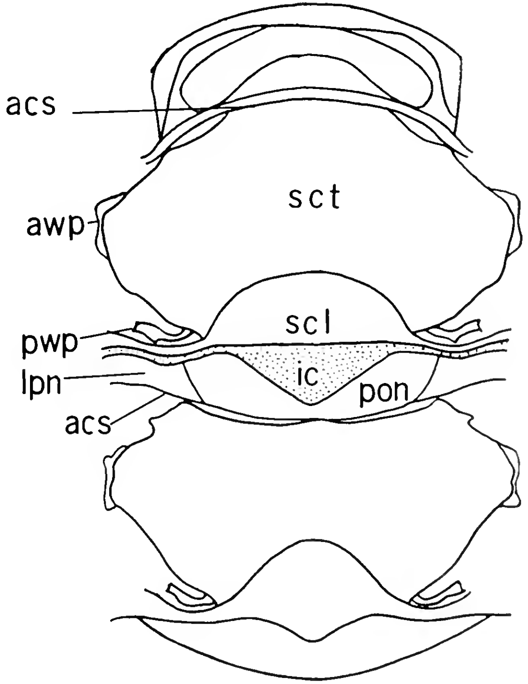

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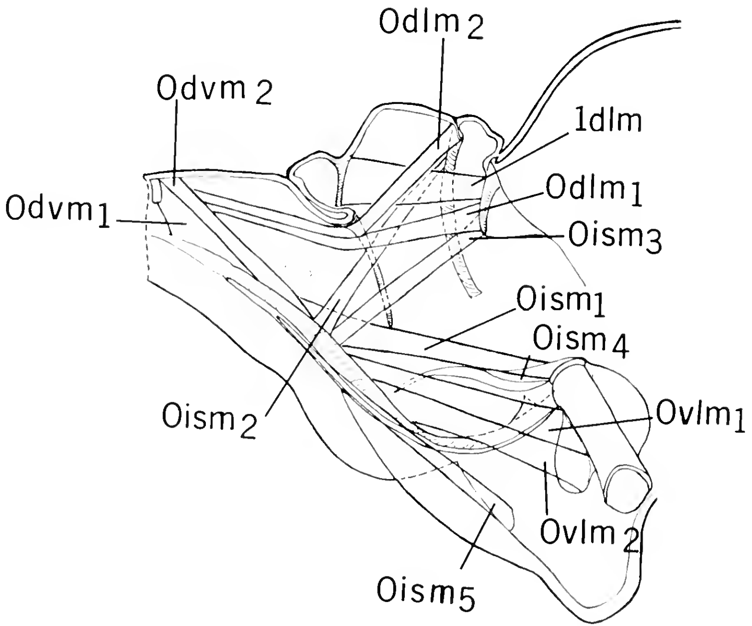

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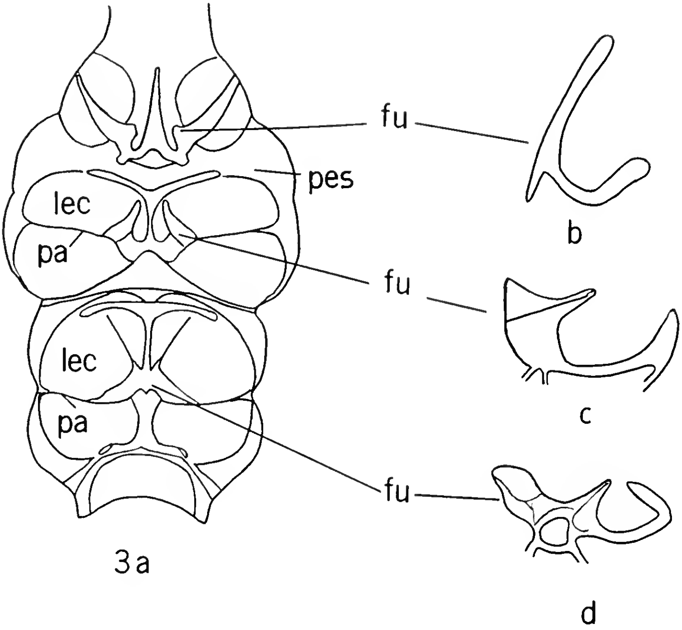
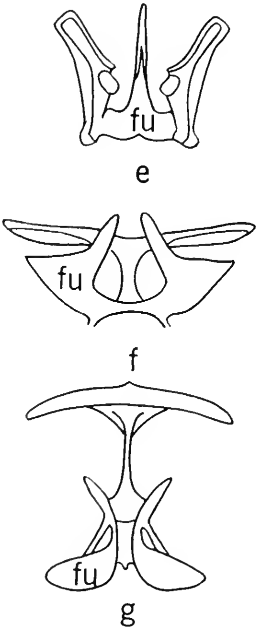
Fig. 1. *Chorista australis.* Dorsal view of the thorax representative of Mecoptera in general.

Fig. 2. *Notiothauma reedi.* Parasagittal view of cervix and pronotum exhibiting the cervical muscles.





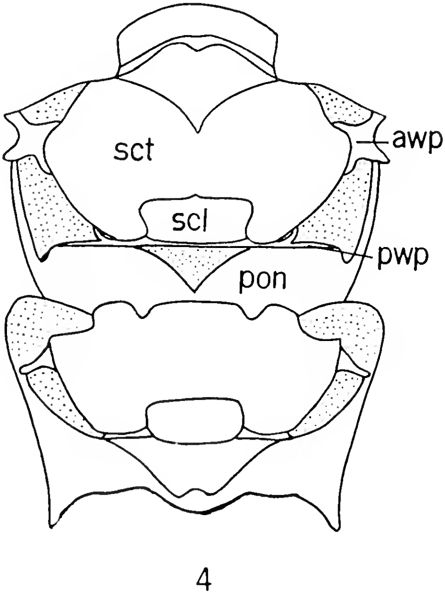
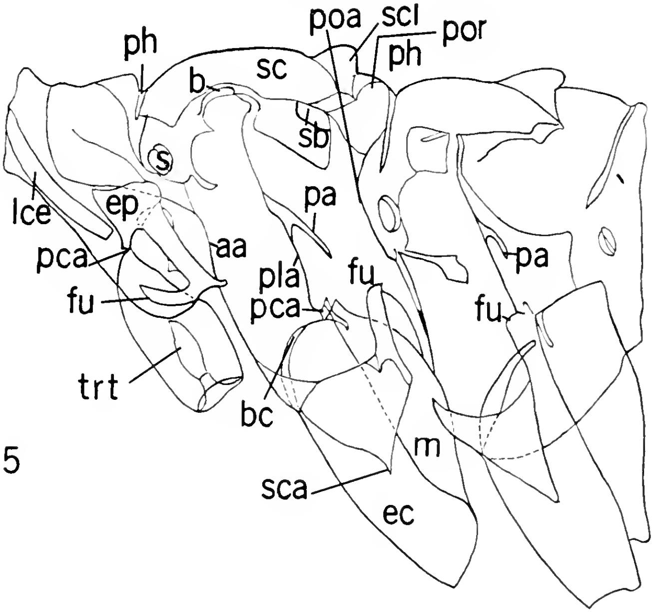


FIG. 3. *Bittacus chlorostima.* a) Dorsal view of sternal region with tergum removed. b-d) Lateral view of the respective furcae. e-g) Dorsal view of furcae alone.

FIG. 4. *Nannochorista maculipennis.* Dorsal view of the thorax.



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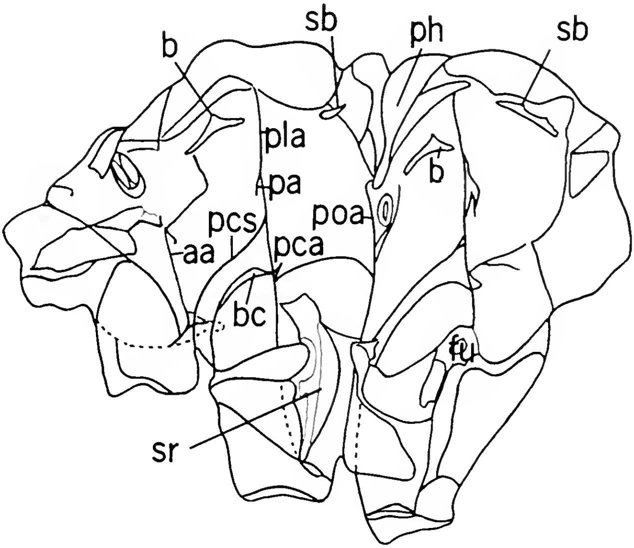

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FIG. 5. *Brachypanorpa carolinensis*. Lateral internal view of the thorax showing the skeletal elements.

FIG. 6. *Bittacus chlorostigma*. Lateral internal view of the thorax showing the skeletal elements.

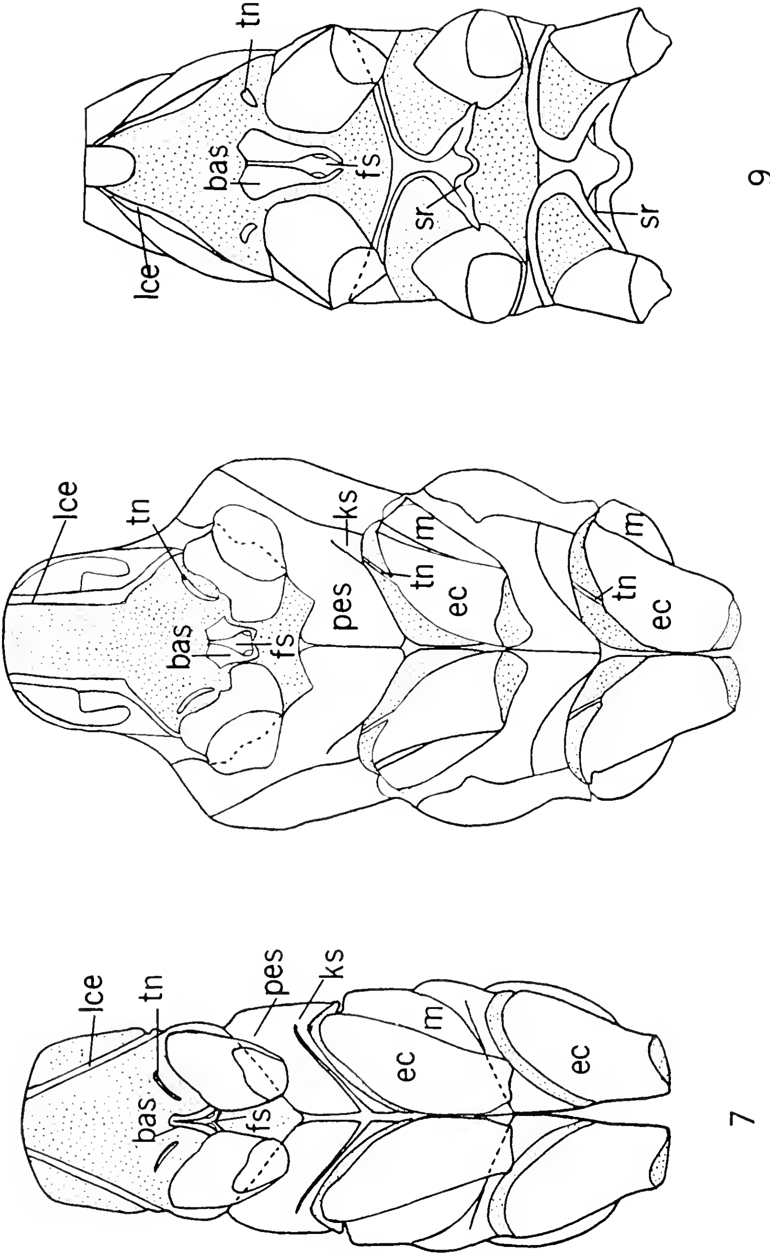
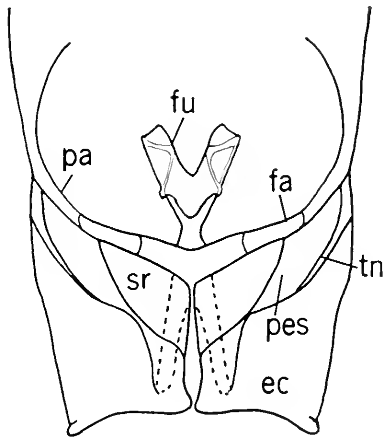


FIG. 7. *Brachypanorpa carolinensis.* Ventral view of the thorax. FIG. 8. *Notiothauma reedi.* Ventral view of the thorax. FIG. 9. *Apteropanorpa tasmanica.* Ventral view of the thorax.



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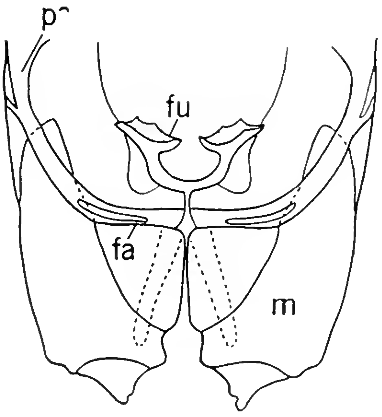

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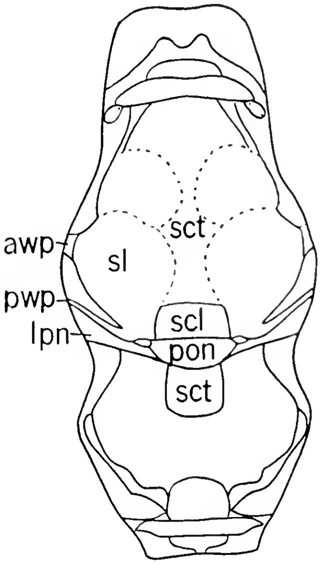

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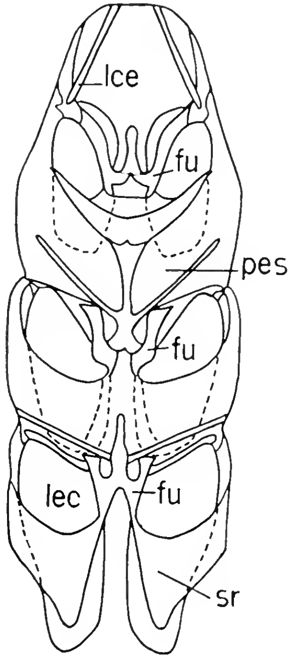

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Fig. 10. *Bittacus chlorostigma.* Anterior view of the skeleton of the mesothorax.

Fig. 11. *Bittacus chlorostigma.* Posterior view of the skeleton of the mesothorax.

Fig. 12. *Bittacus chlorostigma.* Dorsal view of the thorax. Note the absence of any intersegmental conjunctiva. Broken lines indicate humps.

Fig. 13. *Brachypanorpa carolinensis.* Dorsal view of sternal region with tergum removed. Broken lines indicate the continuation of the coxae on the ventral side.

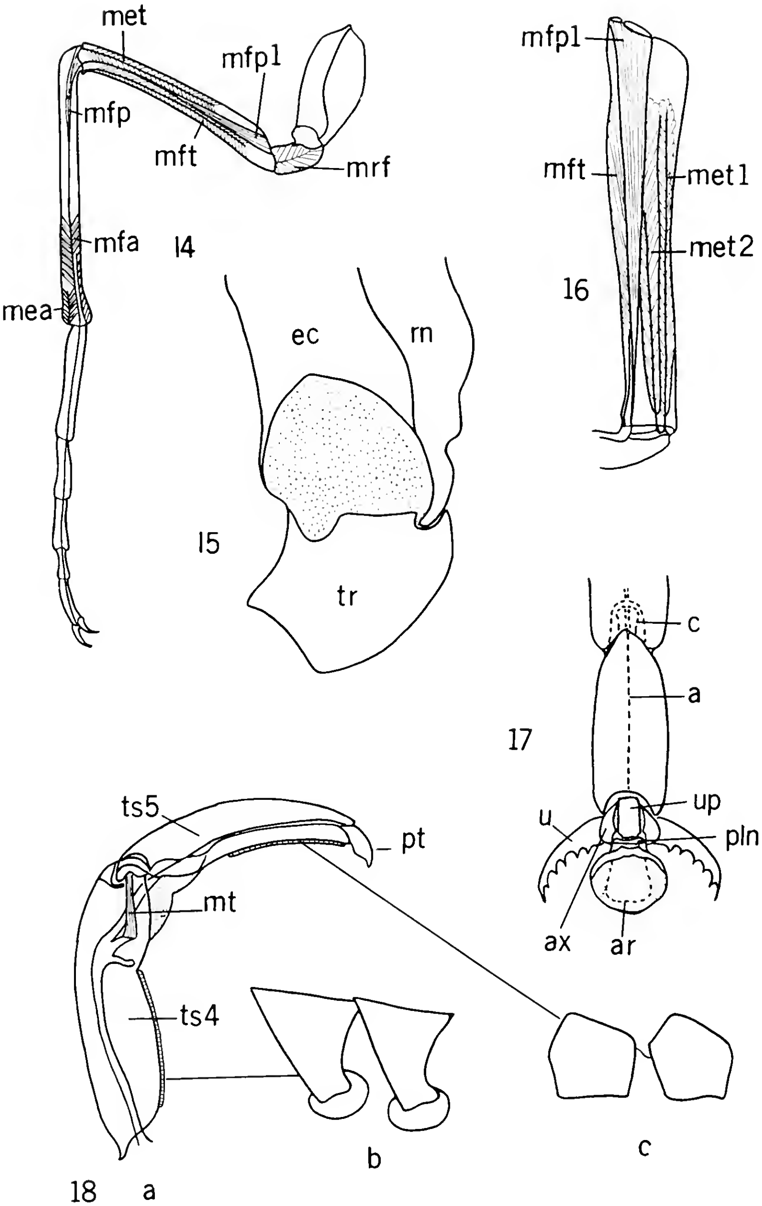


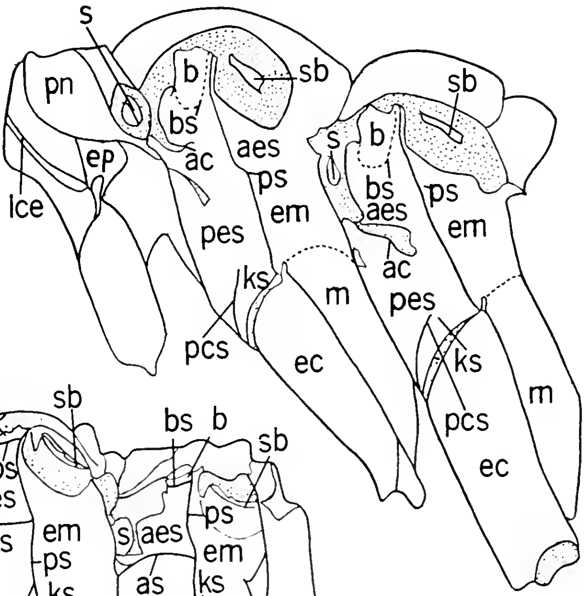
FIG. 14. *Panorpa communis.* View of the leg and its musculature. (Generalized from Hasken, 1939).

FIG. 15. *Notiothauma reedi.* Generalized view of the mesothoracic coxo-trochanteral articulation. Note the role of the meron in the posterior articulation.

FIG. 16. *Bittacus italicus.* Lateral view of the femoral musculature. (Generalized from RÖBER, 1942).

FIG. 17. *Panorpa nuptialis.* Ventral view of the fifth tarsomere and pretarsus, typical of Mecoptera. (Generalized from Ferris and Rees, 1939).

FIG. 18. *Bittacus chlorostigma.* a) Lateral view of the last two tarsomeres and the pretarsus. b-c) Details of the teeth that occur on the inner surface of the tarsomeres.



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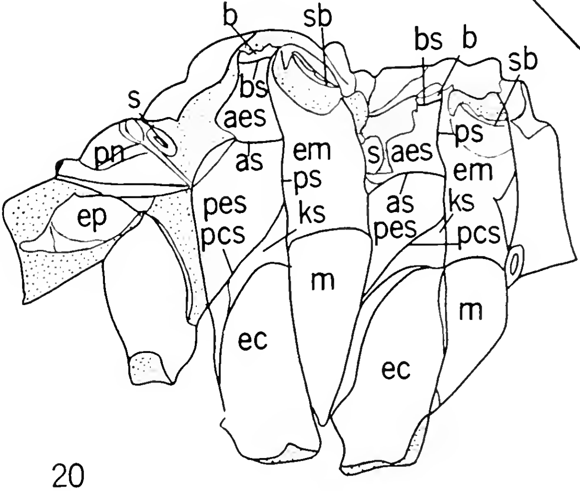

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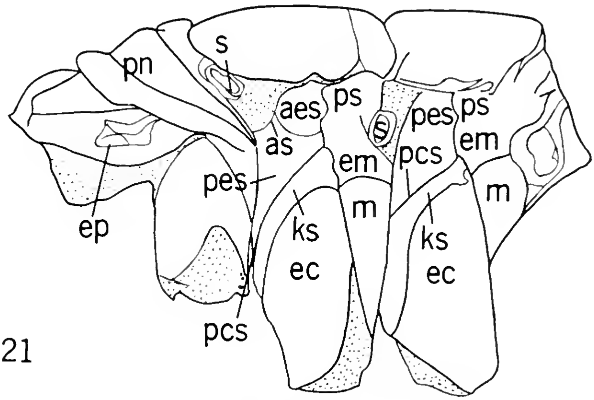

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FIG. 19. *Brachypanorpa carolinensis*. Lateral view of the thorax.
FIG. 20. *Bittacus chlorostigma*. Lateral view of the thorax.
FIG. 21. *Apterobittacus apterus*. Lateral view of the thorax.

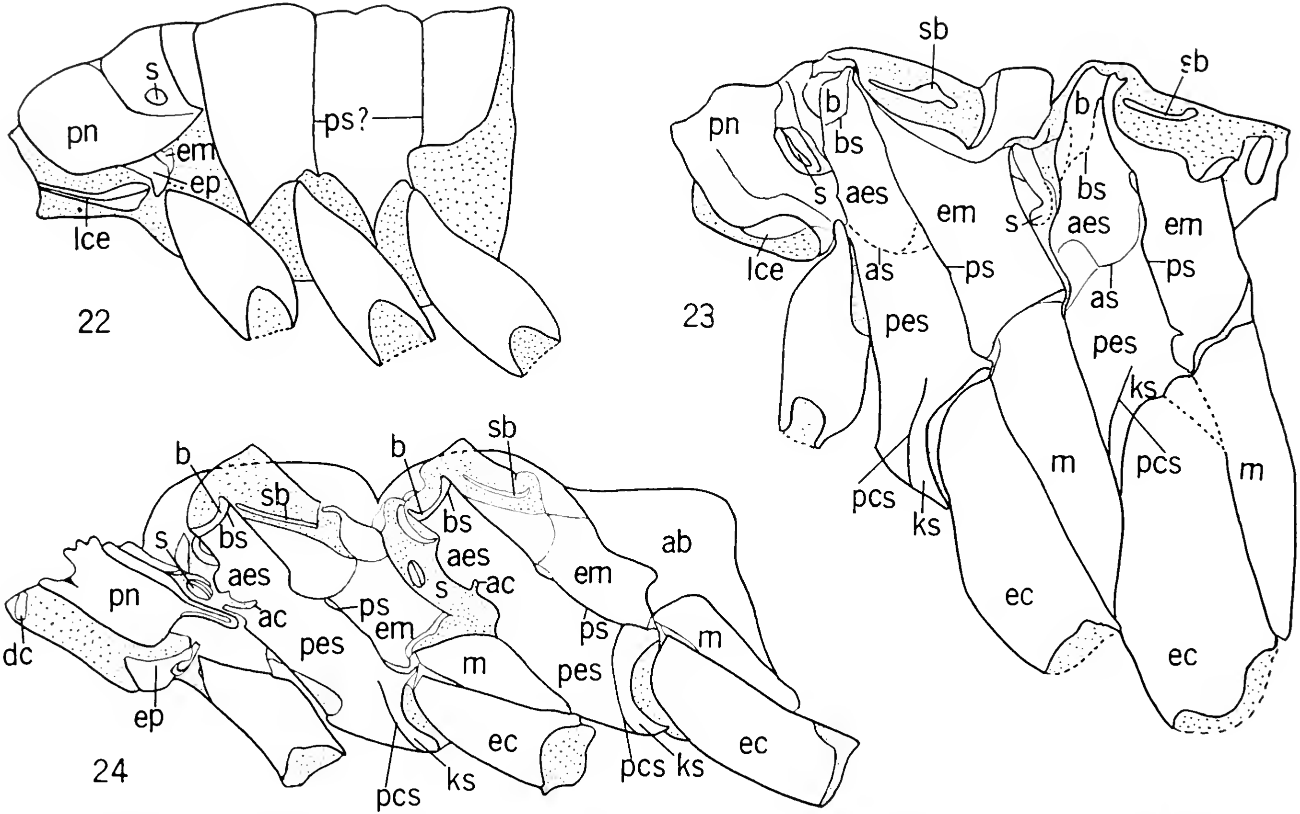
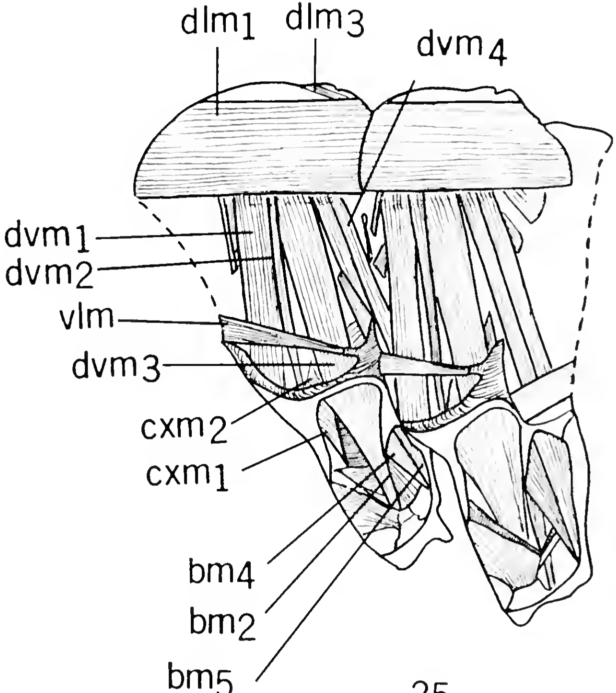


FIG. 22. *Apteropanorpa tasmanica.* Lateral view of the thorax. FIG. 23. *Chorista australis.* Lateral view of the thorax. FIG. 24. *Notiothauma reedi.* Lateral view of the thorax.



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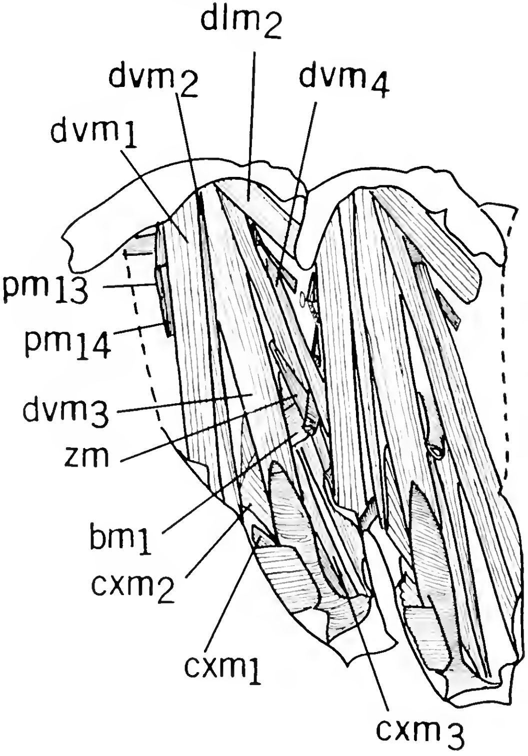

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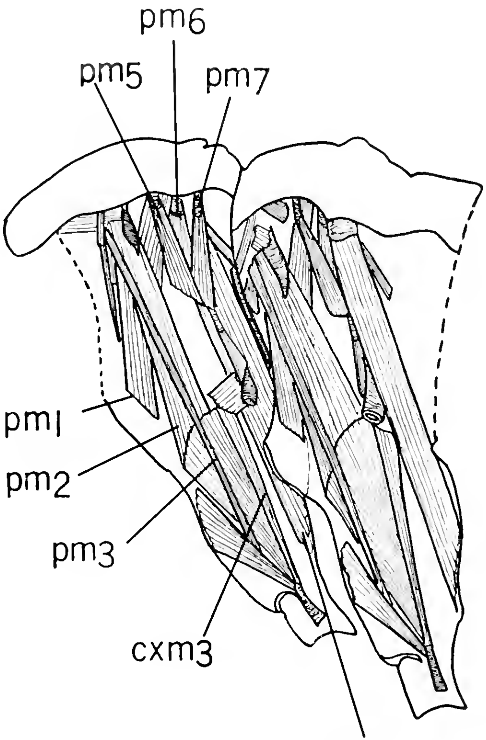
Fig. 25. Generalized pterothoracic musculature (modified from Hasken, 1939), first section, sagittal.
Fig. 26. Same as above, second section, parasagittal.



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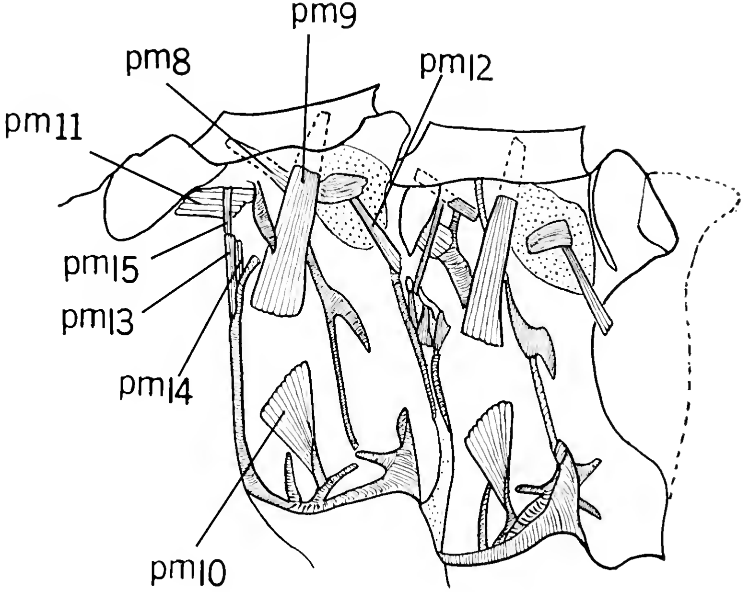

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FIG. 27. Generalized pterothoracic musculature (modified from Hasken, 1939), third section, parasagittal.
FIG. 28. Same as above, fourth section, parasagittal.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVIII Pages 845-848 May 1, 1970 No. 22

An Aquatic Caecilian from the Magdalena River, Colombia, S.A.

Edward H. Taylor*

Dr. Edwin Cooper, of the University of California Medical School, recently sent me a caecilian which he had used in certain experimental work. It appears to belong to the recently described genus *Nectocaecilia* Taylor, a genus comprising four previously known species that are widely distributed in South America. As yet only an exceedingly small number of individuals of this genus have been taken. It is presumed that this species is aquatic, as are the species of the related genera of the family Typhlonectidae.

Nectocaecilia cooperi, sp. nov.

(Figs. 1-2)

Holotype. American Museum of Natural History, No. A82255. From the Río Magdalena at Barranquilla, Colombia, South America.

Diagnosis. Having the generic characters. An elongate slender typhlonectid caecilian lacking a dorsal "fin." Approximately 86 primary folds, some rather dim, seemingly none complete; 96 vertebrae; eyes visible, in socket. Width of body in length approximately 45 times. Dentition in four series. Internal nares very large. Deep black throughout except for light coloration about eyes and at vent, and slightly lighter coloration on the head and jaws.

Description of the Holotype. Head a little wider than body; total length 356 mm. Eye visible, in a socket; tentacular opening very small, close behind the much enlarged nostril, the distance from eye, 4 mm, from nostril 0.45 (the tip of the snout has been injured the skin missing, so that the deeply sculptured bones are exposed). Snout tip to first nuchal groove, 12 mm (lateral measurement), to third nuchal groove, 22 mm. The two nuchal collars are indistinct. Following the collars there are approximately 86 primary folds (some dim and difficult to count), the body with a large unsegmented "shield" at termination. The last centimeter of body strongly triangular in cross section, flattened on the ventral side. The disc of the anal region whitish,

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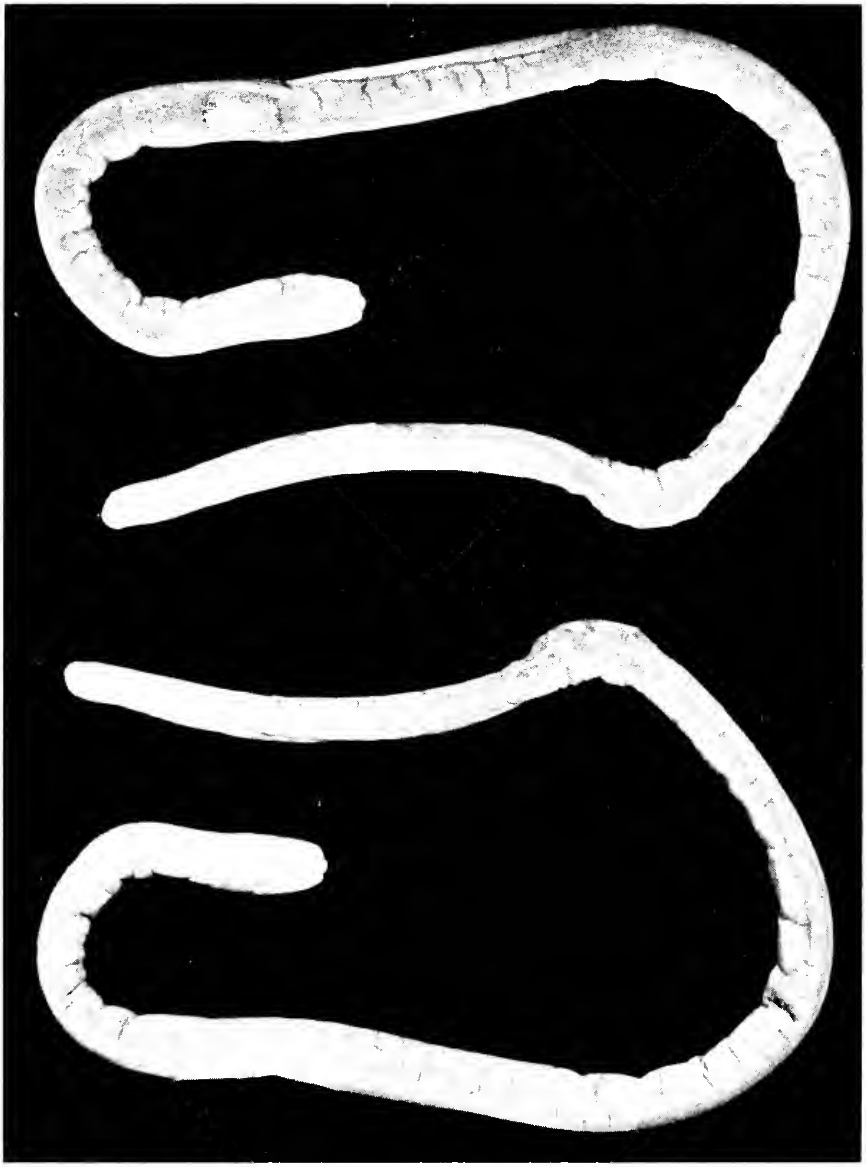

FIG. 1. *Nectocaecilia cooperi* sp. nov. Holotype. AMNH No. A82255. From Río Magdalena, Barranquilla, Colombia, S.A. Dorsal (upper) and ventral (lower) views. Actual length, 356 mm.

somewhat oval, the grooves between the surrounding denticulations terminating at vent, do not reach to edge of disc. There are 5 denticulations posterior to the vent, two lateral to it, each of which bears a small black anal gland, and two larger ones preceding the vent. A vague suggestion of a dorsal ridge but no dorsal "fin." Choanae very large relatively, the length 3 mm, the width approximately 1.5 mm. The distance between choanae, 1.1 mm. No scales or secondary folds. The general surface relatively free from the wrinkles usually present in the typhlonectids.

Dentition. Premaxillary-maxillary series, 18-1-18; prevomeropalatine, 18-1-18; dentary 16-17; splenial series, 3-(1?). The counts, if not exact are very close approximations. The palatine and splenial teeth are the smallest, the anterior dentaries largest.

Measurements in mm. Total length, 356; head width, 9; body width about 8; width preceding vent, 4.4; body height, 8; snout projects 3.

Remarks. A figure of the type specimen is presented. The spine in the posterior part of the body has been broken and healed before capture. An X-ray shows the presence of 96 vertebrae.

The species is presumably related to *Nectocaecilia haydee* (Roze), a species which differs in having a "fin" from head to terminus. The number of splenial teeth is different.

The type is most probably a young specimen. It has been named for Dr. Edwin Cooper who has made the specimen available to me for study.

Fig. 2. *Nectocaecilia cooperi* Holotype. From Río Magdalena at Barranquilla, Colombia, S.A. X-ray showing 96 vertebrae.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVIII Pages 849-854 May 1, 1970 No. 23

A New Caecilian From Ethiopia

Edward H. Taylor*

Two caecilian specimens were sent to the British Museum of Natural History from Ethiopia by Mr. M. J. Largen of the Haile Sellassie I University, Addis Ababa. These in turn have been made available to me for study by Miss Alice G. C. Grandison, Curator of Herpetology at the British Museum.

The first specimen, BMNH No. 1969·1589, was found at Aleku village 12 km N of Dembidollo, Wallega, Ethiopia at an elevation of approximately 1846 m (34° 37′E; 8° 39′N). The second, BMNH No. 1969·976, was obtained by the Great Abbai Expedition, at Ghimbi, Wallega, Ethiopia at an elevation of approximately 2180 m (35° 50′E; 9° 10′N). The latter locality is "no more than 125 km (in direct line) NE of Aleku."

These localities are several hundred kilometers north of previously known points that have yielded caecilians on the eastern side of Africa; however, on the western side they have been taken in southern Senegal some 5° farther north than the Ethiopian localities.

The caecilians seemingly belong to a new species of the genus *Geotrypetes*, and it is herewith described:

Geotrypetes grandisonae sp. nov.

(Figs. 1-4)

Type. British Museum (Natural History) No. 1969·1589, Aleku, 12 km N Dembidollo, Ethiopia, 1846 m elev. Paratype. BMNH, No. 1969·976, Ghimbi Wallega, Ethiopia, 2180 m elev.

Diagnosis. A rather short plump species, reaching a known length of 259 mm. The body width in length approximately 24 times. Eyes visible in a socket not continuous with the tentacular groove. Tentacle distinctly closer to the eye than to the nostril. Primary folds 84-95, complete dorsally but narrowly incomplete on the anterior ventral part of the body. Secondary folds 69-72 with 32-33 complete. Splenial teeth, 3-3 to 5-5. Four to five scale rows in each fold on the last two cm of body. Tongue with two small narial plugs. A diastema between the squamosal bone and the parietal bone.

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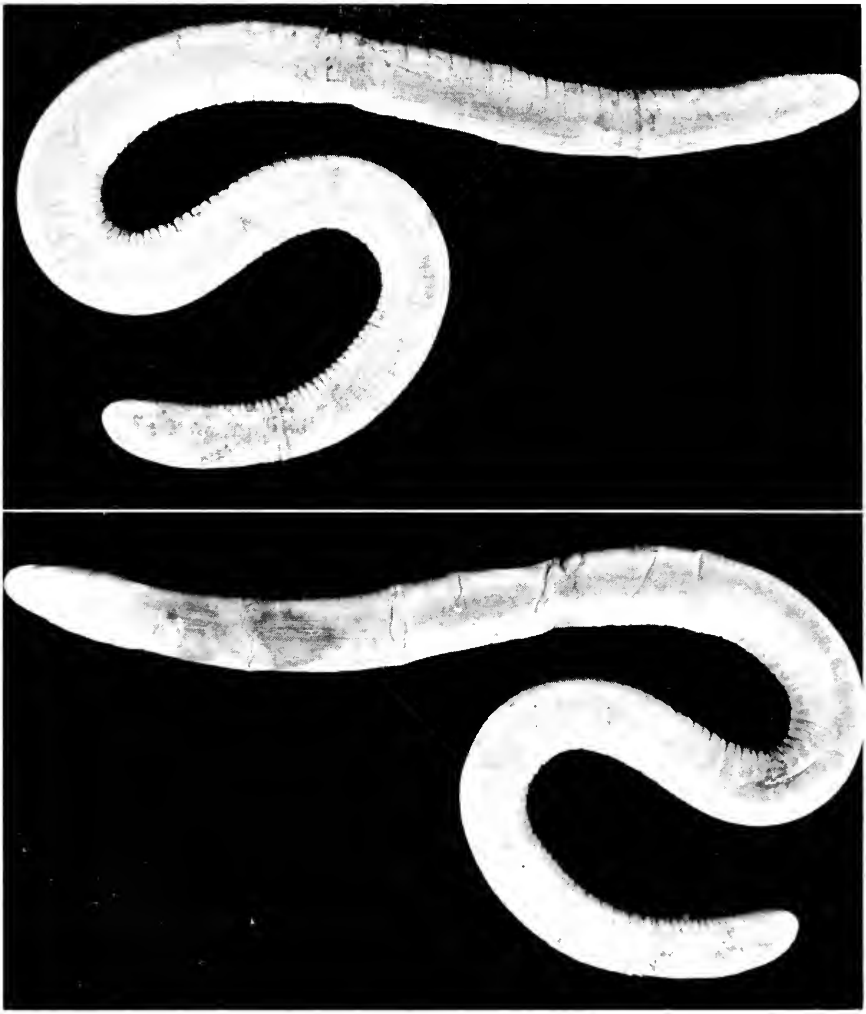

FIG. 1. *Geotrypetes grandisonae* sp. nov. Holotype, (♀ ?) British Museum (Natural History) No. 1969.1589; Aleku, 12 km N Dembidollo, Ethiopia, 1846 m elev. Dorsal (upper) and ventral (lower) views. Actual length, 259 mm.

Descriptions of Type. A small, rather thick-bodied species tapering slightly posteriorly, the length 259 mm, the body width 11 mm; body width in length, approximately 23.5 times. Head narrowing somewhat anteriorly, with rounded snout projecting 1.2 mm beyond mouth; length of lower jaw from tip to rictus oris, 8 mm. Eye in socket which is not continuous with the tentacular groove. Tentacle distinctly closer to eye (1.9 mm) than to nostril (2.7 mm). Snout tip to first nuchal groove, 12.4 mm; to 2nd groove, 15.4 mm; to 3rd nuchal groove, 19 mm (lateral measurements). Tentacle about equidistant between edge of lip and a line from eye to nostril, the external opening minute, somewhat horseshoe-shaped, very slightly elevated. The two collars following occiput not very distinct, seemingly somewhat swollen (perhaps due to a small tumor in mouth and throat). The first nuchal groove distinct laterally, vague dorsally and ventrally; a transverse groove vaguely evident on collar; second groove limiting first collar distinct below and on side but very dim or absent dorsally; the third groove rather distinct dorsally and ventrally, except it fuses with the first primary fold for a short distance. Second collar wider than first, with no dorsal transverse groove evident. Primary folds following second collar, 84, complete dorsally throughout but narrowly incomplete ventrally on most of anterior half of body. Secondary folds, 69, of which about 33 are complete.

Scales beginning on primary folds at a point near first secondaries. At midbody, 2 to 3 scale rows, which may not be complete ventrally, in each fold; posteriorly, 4-5 scale rows in each fold, the scales variable in size, the largest 1.2-1.4 mm in greatest width. No subdermal scales found.

Glands in skin visible, but not especially conspicuous. In the grooves the elongate glands are directed forward and downward but are less conspicuous than in many caecilians. No anal glands visible (♀ ?).

Scales not found in the first secondaries. Terminal "shield" very small (3 mm wide). Vent subcircular, the surrounding denticulations elevated (may not be typical).

Dentition. Premaxillary-maxillary series, 19-1-21; prevomeropalatine, 20-1-21; dentary, 17-17; splenial, 5-5. Dentary teeth for the most part larger than maxillaries or premaxillaries and these in turn larger than prevomeropalatines. The splenials equal to or a little smaller than prevomeropalatines.

Measurements in mm. Total length, 259; head width (greatest), 9; body width (middle third), 11; width near vent, 8.5; vent to terminus, 2; width in length, approximately 23.5 times.

Color. The general color is a dull bluish to violet slate nearly uniform above, perhaps somewhat more violet anteriorly. Top and sides of head and chin more grayish, lighter than dorsum. A distinct light spot over and surrounding eye, one at nostril, one at tentacle, and one covering the denticles in

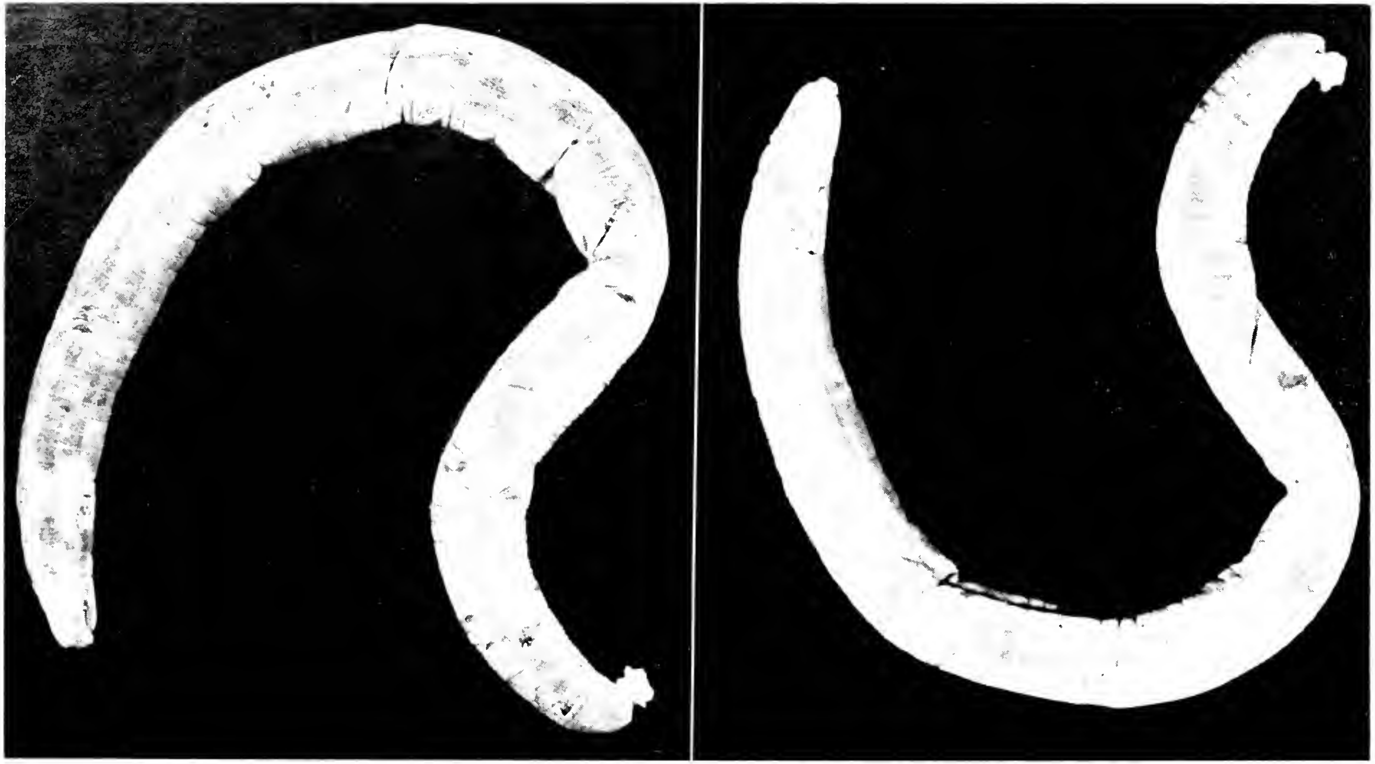

FIG. 2. *Geotrypetes grandisonae* sp. nov. Paratype. ♂. British Museum (Natural History) No. 1969.976; Ghimbi, Wallega, Ethiopia, 2180 m elev. Dorsolateral (left) and ventrolateral (right) views. Actual length, 231 mm.

vent area. Folds on sides have very narrow inconspicuous light edges on anterior part of body.

Remarks. Most of the characters of the skull are unknown. However, there is a diastema between the squamosal and parietal bones and the orbit of the eye is not continuous with the tentacular groove. A tumorous growth is present in the posterior palatal area extending back into the throat. The tongue is swollen as if it too might be affected by the disease. There seems to be only a relatively small passage left for food.

A second specimen (paratype) referred to this species is BMNH No. 1969·976. It offers the following data: primaries, 85; secondaries, 72; complete secondaries 32; premaxillary-maxillary teeth, 20-1-18; prevomeropalatine teeth, 17-1-18; dentary, 15-1-15 (seemingly a median tooth); splenial, 3-3. Measurements in mm are: length, 231 ♀; head width, 7.9; body width, 11.2; tentacle to nostril, 2.1; tentacle to eye, 1.7.

The specimen has much the same general color as the type save that the anterior section of the body is darker in places probably due to air exposure and slight dehydration. The penis is partially extended. The collars are very clearly delineated, the second seemingly not fusing below with the first primary fold.

While the two specimens appear to agree in most easily observable characters, there seems to be variation in the secondaries and in scales. I cannot find any scales in the first few secondaries; elongate skin glands are present bordering the folds above, filled with a white cheeselike material. These glands also appear in the primary folds in the same region but here there may be a few scales. Posteriorly, scales appear in both primary and secondary folds, and are similar to those in the type.

On the external surface one may discern certain larger skin glands that may be diseased or possibly the result of parasitism. These contain much cheeselike material. Occasionally some are seen in which the cheeselike material appears to have shrunk leaving a round shallow depression on the surface above it.

The placing of this species in *Geotrypetes* is tentative. It would appear to agree more closely to this than to other African genera. It differs specifically, however, from other known species of this genus in the number of scale rows in the posterior folds, and in that it has fewer splenial teeth, fewer primary folds and a larger number of secondary folds, many of which are complete, and the tentacular aperture is distinctly closer to the eye than to the nostril. Usually the aperture maintains a fixed position within a genus with relation to the eye and nostril.

The species is named for Miss Alice G. C. Grandison who has been helpful in providing these specimens for study.

FIG. 3. *Geotrypetes grandisonae* sp. nov. Terminal view of the partially extruded penis of No. 1969.976, paratype.

FIG. 4. *Geotrypetes grandisonae* sp. nov. Holotype. British Museum (Natural History) No. 1969.1589. X-ray showing 87 vertebrae and relatively long ribs. Total length 259 mm.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVIII Pages 855-860 May 1, 1970 No. 24

Notes on Brazilian Caecilians

Edward H. Taylor*

A small collection of caecilians from Duke University, sent to me by Dr. Joseph R. Bailey, contains four specimens representing three species. Two species are examples of rare, recently described forms. The third is a well-known species of wide distribution. All seem worthy of comment. I have also examined a specimen of the recently described *Nectocaecilia ladigesi* Taylor, and include it here also.

Siphonops paulensis Boettger

(Fig. 1)

Siphonops paulenis Boettger, 1892, Katalog der Batrachier-Sammlung in Museum der Senckenbergischen Naturforschenden Gesellschaft, pp. 62-63 (type-locality São Paulo, Brasil).

The specimen, Duke Univ. No. 9628 from Barra Bonita, São Paulo measures (in mm) 291 in length, body width about 25, head width 16, terminal "shield" width 20, and a circumference of 82. The length divided by width is approximately 23.6. The primary folds are 104, the vertebrae 108 or 109. The color is a typical dark bluish slate, each fold marked laterally and ventrally with white lines which on the back become dulled and greatly narrowed so that they are not or scarcely discernible. Anal glands are present (♂).

This, I believe, is the largest known specimen of this species.

A smaller specimen, Duke Univ. No. A 9629, is from Jarimu, near Jundiaí, São Paulo. This has 109 primary folds, and a length of 251 mm.

The range of this species is chiefly in eastern and southeastern Brasil. Specimens are known from the States of Rio Grande do Norte, Bahia, Minas, Gerais, Espírito Santo, Guanabara, São Paulo, Rio Grande do Sul, Southern Goiás and southern Mato Grosso; also from northern Argentina, Paraguay and Bolivia.

Specimens from Goiás seemingly have the lowest number of primary folds, the four specimens examined having counts of only 101-104. The known range of counts elsewhere is 104-119 folds.

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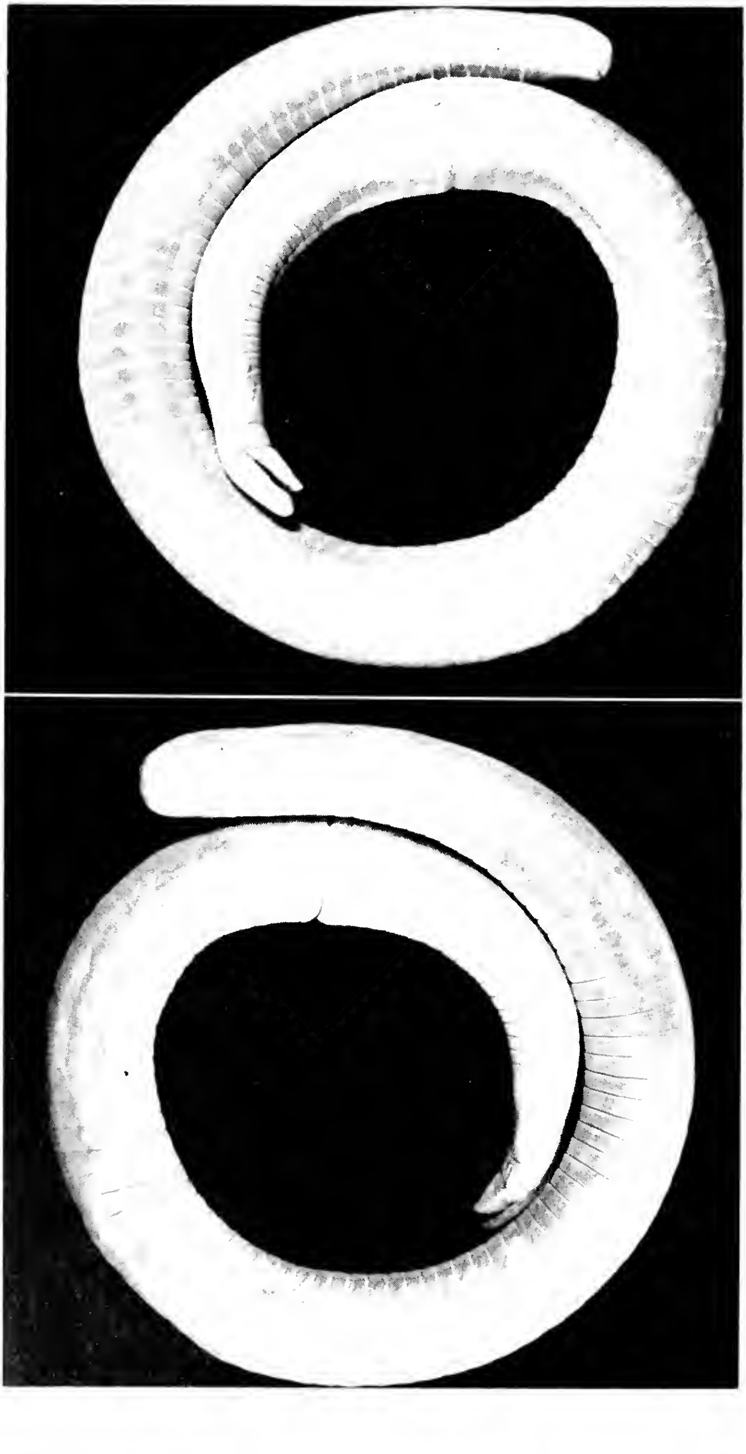

FIG. 1. *Siphonops paulensis* BOETTGER. Duke Univ. No. A 9628, Barra Bonita, São Paulo, Brasil. Total length, 291 mm; body width, greatest, 25 mm.

This species, like *S. annulatus,* is adapted to relatively dry situations, and like that species has a wide distribution. However, it appears to be confined to the drainage areas of the Río Paraná and the short coastal rivers emptying into the Atlantic, while *annulatus* has a far wider range, extending into western and northern South America.

Oscaecilia hypereumeces Taylor

Oscaecilia hypereumeces Taylor, 1968, The Caecilians of the World, pp. 607-611, figs. 331-334 (type-locality, Joinville, Santa Caterina, Brasil).

This specimen, Duke Univ. No. A 9627 (locality unknown), the second known of this species, has the following characters:

The eye is present under bone, the tentacle almost directly below the nostril, very much closer to nostril than to eye. The scales begin near the middle of the body, only a few in a fold laterally. More posteriorly there is a single row of scales around the body with occasionally one or more extra scales appearing dorsolaterally. The elongate glandules lying above the scales seemingly are more numerous than the scales.

Its counts and measurements are as follows; numbers in parentheses refer to the type: The primary folds, 208 (226) are incomplete above and below except in the posterior part of the body. There are 21 (4) secondaries of which 6 are complete. There are four dental series (the tooth counts, if not correct, are close approximations): premaxillary-maxillary, 10-1-10 (8-1-7); prevomeropalatine, 11-1-11 (10-1-9); dentary, 10-10 (9-9); splenial, 2-2 (3-3).

Measurements in mm. Total length (body broken), approximately 400 (640); body width, 5 (7); snout projects 1.8 (1.9); tentacle to eye, 2.6; tentacle to nostril 1.1 (1.0); tip of snout to angle of jaw, 5.2; tip of snout to first nuchal groove, 7.2, to second groove, 9.1, to third, 11.5 (all lateral measurements); width in length, approximately 80 (91) times.

Remarks. The head is whitish to light brown from the eyes forward to near the tip of the snout, with light areas about nostrils and tentacles. A cream spot is present posterior to the brown area. A pair of brownish spots is behind and above jaw angle, in front of which is an indefinite light lateral streak. The edge of the upper lip is light with a vaguely darker streak above. The entire lower jaw is whitish or cream but with a fine scattering of darker pigment. The anterior 10 cm of the body is an ill-defined violet brown, the venter a dull cream with a thin scattering of pigment. Posterior to this, the body is variegated vaguely (suggested in the figure of type, no. 331, *loc. cit.*) and brown in color. In practically all other characters this specimen agrees with the type.

The differences in the count of primaries and secondaries from those of the type are not greater than has been reported in several species of *Caecilia.*

An x-ray picture of this specimen prepared by Dr. Joseph Bailey shows 214 vertebrae. The subdermal scales are scattered and difficult to find in the

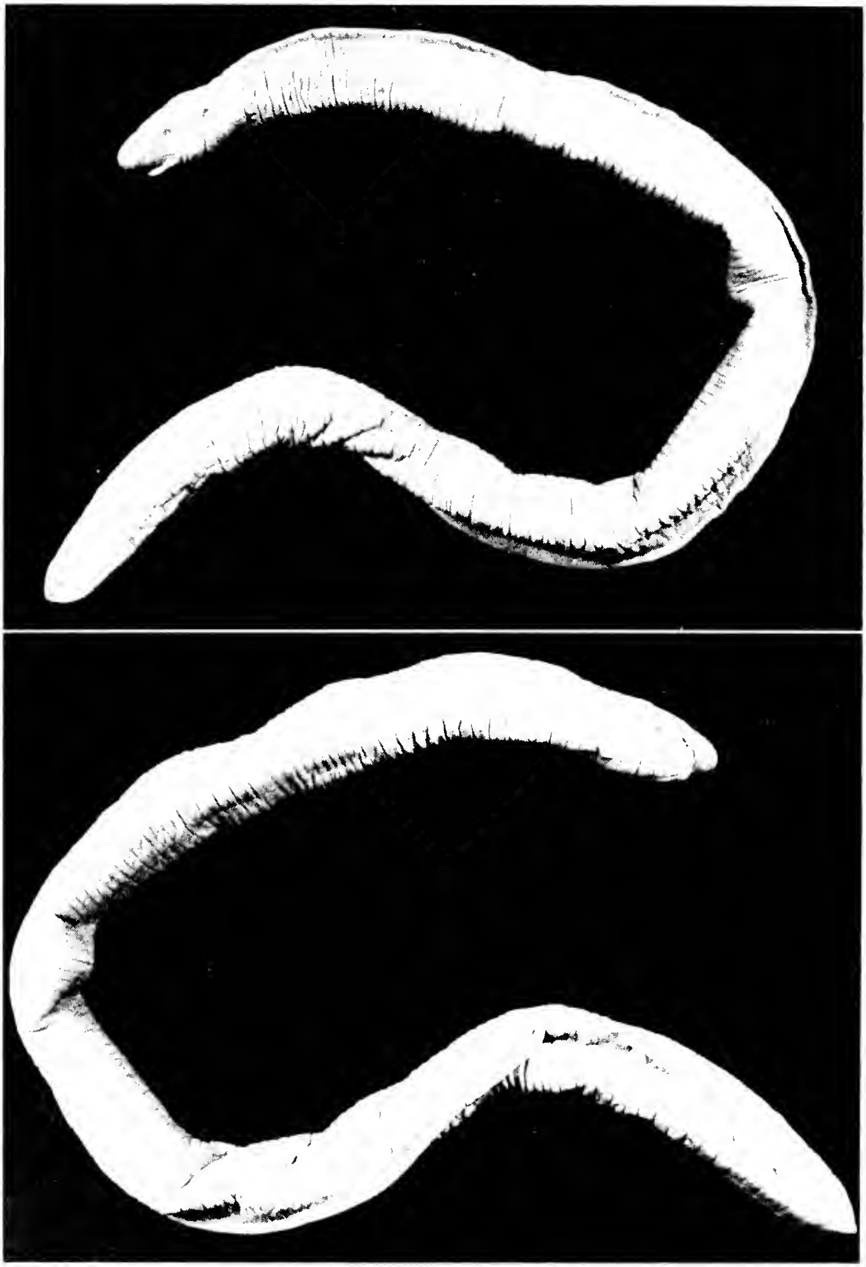

FIG. 2. *Typhlonectes anguillaformis* Taylor. Duke Univ. No. A 9630. "Probably vicinity of Manaos," Brasil. Total length, 372 mm; body width, approximately 19 mm.

thin connective tissue under the skin. They are small, circular and nearly transparent, usually less than .5 mm in diameter. Posteriorly some of the scales in the grooves are vaguely visible externally along sides.

Typhlonectes anguillaformis Taylor

(Fig. 2)

Typhlonectes anguillaformis Taylor, 1968, The Caecilians of the World, pp. 235-238, figs. 117-120 (type-locality unknown).

This specimen, Duke Univ. No. A 9630, is in good condition except that a portion of the side of the snout has been dissected. The color has become almost uniform light brown; presumably it originally was some shade of slate or violet. The type specimens are somewhat grayish but I believe that this is not the color in life, since when the loose epidermis was removed, the color below appeared violet-brown. Since this is the third known specimen, I am recording the following data:

The head is short and somewhat flattened. The body length is 373 mm, its width approximately 19 mm, the head width, 13.6 mm. The width in length is approximately 19.6 times. The minute tentacle is close (0.7 mm) behind the large nostril. There are 82 primary folds and no true secondaries. Most folds have at least one transverse crease or wrinkle. There is an unsegmented terminal "shield," triangular in cross section. The subterminal area is bounded laterally by two slightly sinuous ridges extending forward for about 3 cm. These are slightly more compressed than is depicted in the figure of the type (Taylor, *loc. cit.*, fig. 119).

The dorsal skinfold (fin) begins at the second collar and continues to the terminus. At first it is about 2 mm high, becoming gradually higher posteriorly, and reaching a height of 6-7 mm on the last 2 cm of the body. The tentacular opening is minute and is not evident in the type figure (*loc. cit.*, fig. 119).

In practically all other characters the specimen agrees with the type.

Nectocaecilia ladigesi Taylor

(Fig. 3)

Nectocaecilia ladigesi Taylor, 1968, Caecilians of the World, pp. 275-279, figs. 139-142 (type-locality, Rio Moju near its mouth, [junction with the Tocatins] near Belém, Brasil).

A recent acquisition of the U.S. National Museum (No. 154035) is a specimen of the above species, collected by Dr. Philip Humphrey in 1964 at Utinga, Belém, Brasil. Data on the specimen are as follows: numbers in parentheses are those of the type*; measurements are in mm: length, 389 (416); head width, 12 (13); neck width near the head, 8.8; greatest body width, 14 (9.5); height of body, 18.5 (17); width at vent, 5.3. There are 92 (97) vertebrae.

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* In the type description, p. 277, line 4, for "6" read "9.5"; p. 279, line 12, for "eye" read "tentacle."

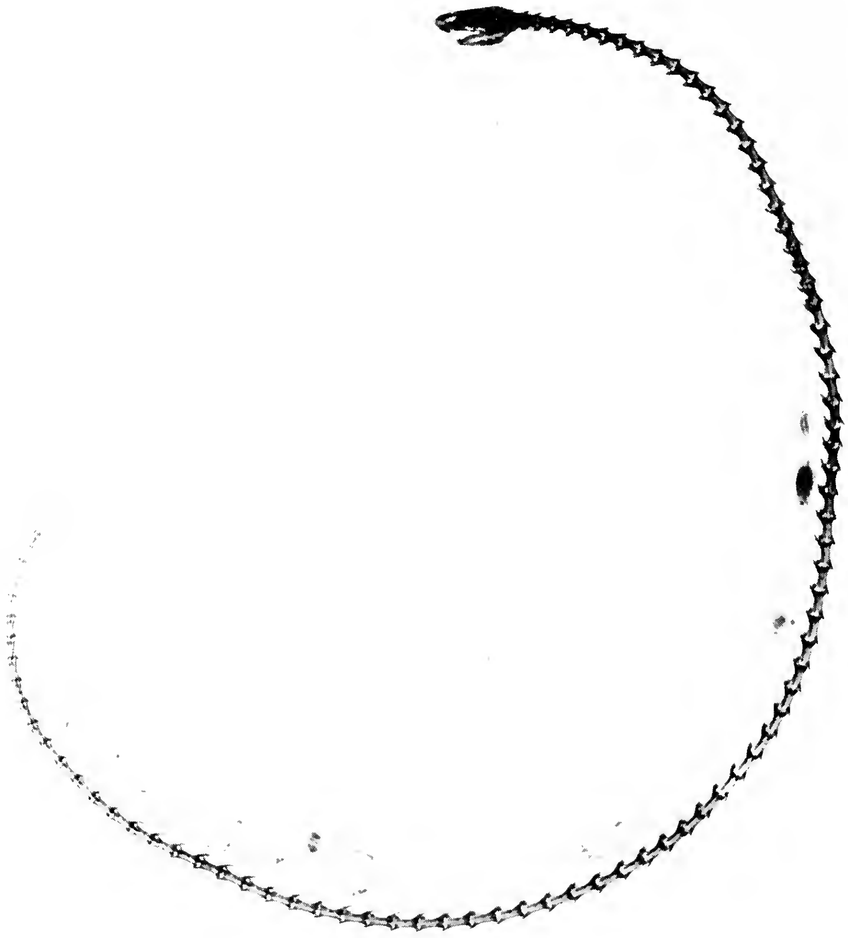

FIG. 3. *Nectocaecilia ladigesi* Taylor. USNM No. 154085, Rio Moju near its mouth, near Belém, Brasil. X-ray showing 92 vertebrae. Total length 389 mm.

The counts of the dental series are close approximations of the actual tooth numbers: premaxillary-maxillary, 20-1-24 (19-1-20); prevomeropalatine; 20-1-20 (20-1-20); dentary, 19-18 (17-16); splenial, 6-7 (5-5). The skin is very smooth, the color nearly uniform brownish slate. The denticles surrounding the vent (11 in number) are almost identical in arrangement and proportionate size to those of the type.

I am under obligation to Mr. R. A. Tuck, Jr. of the U.S. National Museum for an x-ray (Fig. 3) and 6 photographs of this, the second known specimen of this aquatic species.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVIII Pages 861-868 May 1, 1970 No. 25

The Lateral-line Sensory System in the Caecilian Family, Ichthyophiidae (Amphibia: Gymnophiona.)

Edward H. Taylor[1]

The sense organs commonly known to anatomists as the lateral-line or neuromast system developed in early aquatic Chordata (Ostracoderms) and continued to appear in subsequently developed aquatic groups. It was a sensory system believed to serve the organism in adjusting to an aquatic environment. When an aquatic animal having such a system changes to a terrestrial environment, the system seemingly no longer functions and tends to disappear. This is true of certain species of fish that assume a semiterrestrial habitat (Symbranchidae). It is also true of many Amphibia that have a free-swimming larval period after hatching and which, at transformation from larval to adult form, usually assume a terrestrial habitat. The system is present in numerous Caudata during the larval period. One species of the genus *Taricha* is said to lose the system on transformation to a land habitat. Later in life when it again resumes the aquatic habitat the system reappears and presumably again functions! Most Salientia that have a free-swimming larval period seek a terrestrial habitat on transformation and the system is lost. However, in certain species that are, as adults, semiaquatic, the system may be partially retained *(Rana hexadactyla* and *R. cyanophlyctis).* Others may remain permanently aquatic and retain more of the system *(Xenopus).*

The neuromast organs of the lateral-line system are usually described as groups of sensory cells, each having a hairlike process at its free end and surrounded by supporting cells. These organs are arranged in series that follow the nerves. They are in pits or depressions in the skin which are usually connected by canals filled with a mucous secretion. The series are symmetrically arranged on the two sides of head and body. In most fishes there is a series crossing the head that connects the two sides. If this is present in the caecilians, it is not obvious externally.

The purpose of this paper is to inquire into the character of this sense system in the third order of the Amphibia, the Gymnophiona, especially in

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the family Ichthyophiidae, and to demonstrate that the general pattern occurring in the Asiatic genera is duplicated in a South American genus of the family.

In the order Gymnophiona, Taylor (1968, 1969) recognized four families: the Ichthyophiidae, Scolecomorphidae, Typhlonectidae and Caeciliidae. The fourth family was divided into two subfamilies, the Caeciliinae and the Dermophiinae.

This sense organ was first reported in Gymnophiona by the Sarasins, who found it in *Ichthyophis glutinosus* (1887a,b). They discuss the system (Seitenorgane) and present figures representing the general distribution of the organs (1887a, pl. 5, figs. 42, 51-54); their structural details are discussed and figures are given (1887b, pl. 6, figs. 11-18). Taylor (1960, 1968) has given figures illustrating the general pattern of the cranial part of the system in *Ichthyophis mindanaoensis, I. youngorum* and *I supachaii.* The first two species have a larval life lasting one or two years, during much of which time the lateral-line system is retained. The third species has a larval life of only a few weeks. At the end of this time the animal transforms and the system is lost as it becomes terrestrial in habitat.

Four genera are recognized. Besides the Asiatic *Ichthyophis,* there is another Asiatic genus, *Caudacaecilia,* and two South American genera, *Epicrionops* and *Rhinatrema.* Larvae of *Caudacaecilia weberi, C. larutensis* and *C. asplenia* have been examined, all showing traces or parts of the system but none showing it satisfactorily, probably because none was of proper age. It is most probable that the details when found will differ but little from those of *Ichthyophis.*

The characteristics of the system in *Ichthyophis* both in the diagram (Fig. 1) and in the retouched photograph (Fig. 2) may be described as follows: On the dorsal surface of the head two lines of neuromasts, seemingly a continuation of the premaxillary series, pass up over the tip of the snout and form two short groups that terminate back of the level of the nostrils. These are designated *internasals.* Just back of the nostrils the *canthals* begin, curve outward and turn backward. They may be somewhat continuous with the *supraorbitals* that curve above the eyes and terminate slightly above and behind the eyes. Below the nostrils, beginning on the upper lip, is the *infraorbital* series that passes up toward the eye, then curves under it and terminates behind the eye but at a higher level. Beginning somewhat back of the eye and running diagonally to near the level of the line of the mouth is the *genal* series. Farther back and about on a level with the mouth are the *supraspiraculars* terminating above the anterior edge of the open gill slits. Beginning on the lower lip are the *mentals* that curve back on the chin to near the level of the corners of the mouth, their terminal points near to each other.

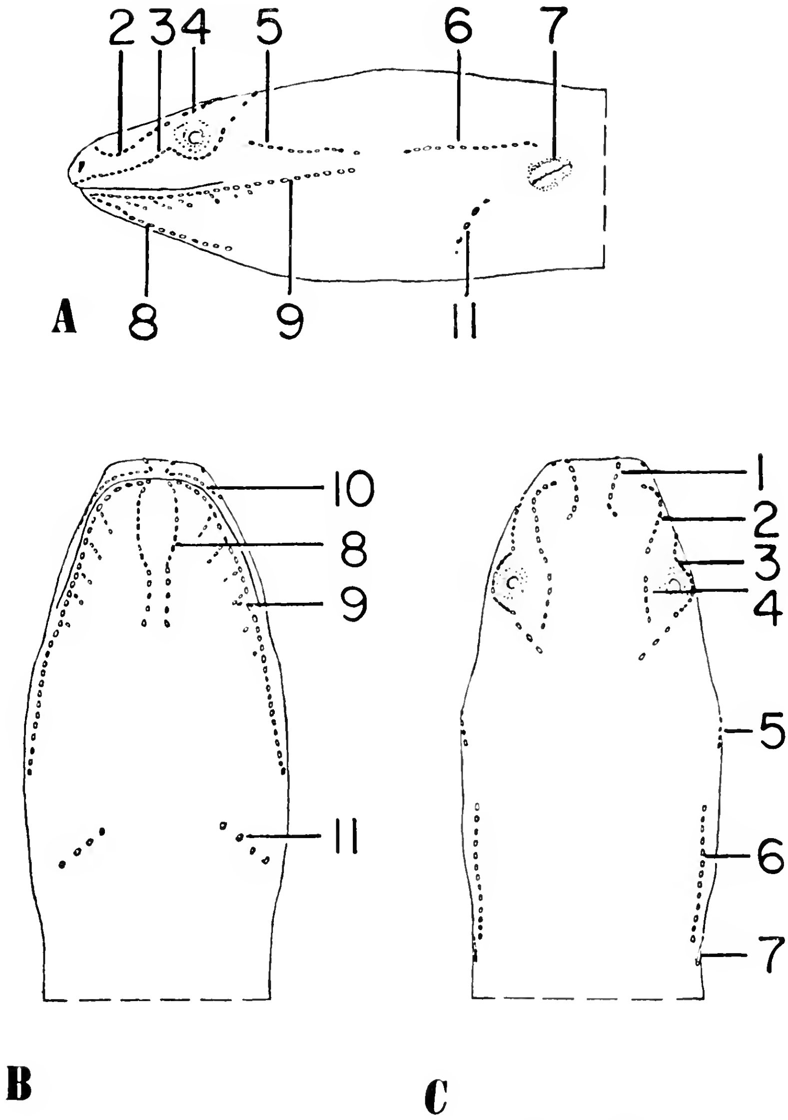

Fig. 1. Neuromast series based on the larval head of *Ichthyophis*. Lateral (A), ventral (B) and dorsal (C) views: 1. internasal series; 2. canthal; 3. infraorbital; 4. supraorbital; 5. genal; 6. supraspiracular; 7. gill slits; 8. mental; 9. infralabial; 10. premaxillary; 11. gular. The three body series are not indicated in the diagrams.

Bordering the lower lip the *infralabials* extend directly backward to near the posterior terminus of the *genal* group. From this series short branches extend backward and inward for a short distance, there being one to three neuromasts visible on each branch. On the beginning of the neck short

Fig. 2. Head of *Ichthyophis peninsularis* Taylor. Larva. E.H.T.-H.M.S. No. 1836, Bangalore, India. Head width, 5.1 mm; total body length, 140 mm. Retouched. Usually the neuromasts appear whitish. This color may disappear before the neuromast is lost.

groups of neuromasts extend back to near the front level of the gill slits. These are designated the *gulars*.

While not shown in the cranial diagram, there are three lines of neuromasts on each side of the body that reach from the gill region to, or near to, the end of the body. They are designated the *upper, middle* and *lower lateral* series. Only rarely are all three visible at the same time on a specimen. It is quite possible that there are other parts of this system which are not obvious to the eye and which might be discovered by histological methods.

The characteristics of the lateral-line system, as seen from the lateral and ventral aspects of *Epicrionops p. petersi*, is best shown in Figure 3. The infraorbital series is nearly complete, as is the genal. The mentals, beginning near the middle of the lower lip, extend back behind the angle of the mouth, more or less contacting the genals posteriorly. Ventrally the infralabials show the numerous short branches to a greater or lesser degree, behind which the mentals may be distinguished. In this species the neuromasts appear distinctly larger and perhaps fewer than in *Ichthyophis* (Fig. 2) and differ somewhat in their general arrangement from that in the diagrammatic Figure 1. The neuromasts on the dorsal surface of the head (Fig. 3) are relatively indistinct,

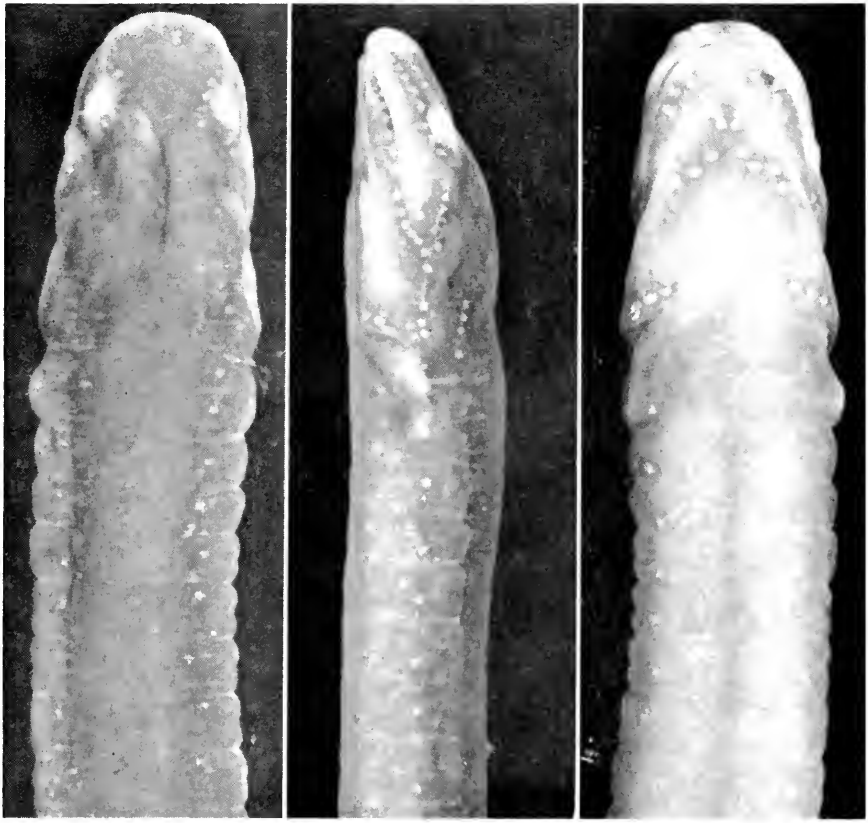

FIG. 3. *Epicrionops petersi petersi* Taylor. Larva. KUMNH No. 119402 (three views of head). Head width, 4.6 mm; total length of specimen, 117 mm. Cordillera del Dué, above Río Coco, 1150 m elev., Napo, Ecuador.

which suggests that they are already tending to disappear. The three linear lateral series are more or less evident, continuing most of the length of the body. Four other specimens of *Epicrionops* (Figs. 4, 5) are shown. What might be regarded a variation is, most probably, only the degree of loss of the neuromasts in older specimens that are preparing to assume the adult characteristics. Measurements recorded suggest that the specimens differ in age and in the degree of development.

In conclusion, insofar as the genera *Ichthyophis* and *Epicrionops* are concerned, one may state that the lateral-line sense organs follow the same general design and the function may be presumed to be the same. Such slender evidence as is available shows that the system in *Caudacaecilia* follows the characteristics of those of *Ichthyophis*. *Rhinatrema*, the most aberrant genus of this family, may or may not be similar. Only two specimens of that genus are known, both adults.

TABLE 1. Data on *Epicrionops p. petersi* Taylor.

Number	119399	199397	119400	119398	119401	119402
Total length	150	135	135	125	125	117
Head width	7	6.1	6	5.1	6	4.6
Tail length	8.1	8.2	9	8	5.2	7.5
Body folds	Total circa 234	Primary circa 64	Total circa 231	Primary circa 66	Primary circa 65	Primary circa 66
Tail folds	13	11	11	11	?	?
Premax-max teeth	12-1-13	12-1-12	11-1-11	10-1-11	10-1-9	11-1-11
Prevom-palatine	17-1-12+	18-1-18	17-1-18	16-1-17	17-1-17	15-1-15
Dentary	13-13	13-14	13-14	12-12	15-1-15	14-1-15
Splenial	5-5	6-7	5-5	5-5	6-6	6-5
Gill-slit	1	1	1	1	1	1
Neuromasts						
Internasal series	-	5-4	5-5	4-5	..	..
Premaxillary	0	0	0	0	0	0
Supraorbital	4-4	5-5	5-5	4-4	5-5	5-4
Infraorbital	12-12	13-14	13-13	14-14	13-13	13-13
Infralabial	18-18	16-18	17-18	16-16	20-19	18-17
Supraspiracular	4-3	6-4	6-6	3-3	4-6	3-3
Genal	2-3	3-4	3-3	3-3	3-3	3-3
Mental	4-4	4-4	4-4	3-3	3-3	3-3
Lateral (middle)	22	21-20	25	20	20-25	18-?

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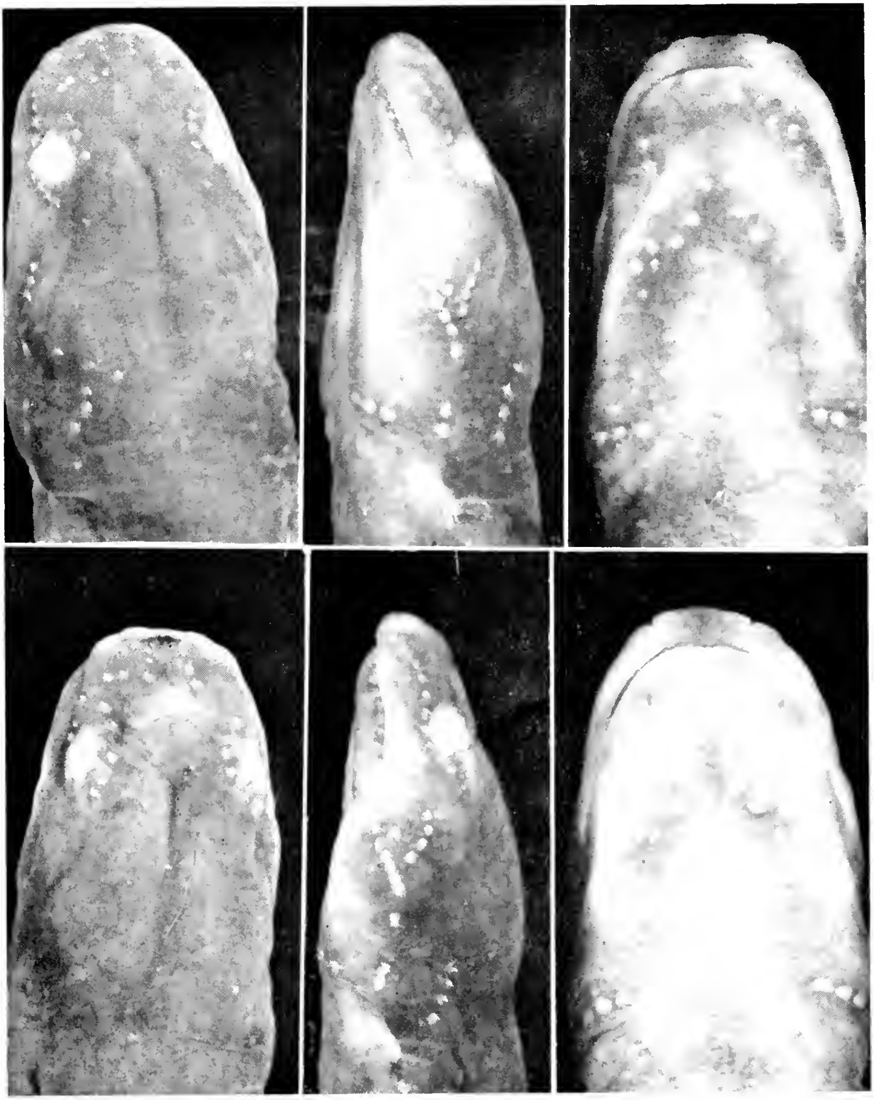

FIG. 4. *Epicrionops petersi petersi* Taylor. Larvae. Upper figures (three views of head), KUMNH No. 119398. Head width, 5.1 mm; total length of specimen, 125 mm. Lower figures (three views of head), KUMNH No. 119401. Head width, 6 mm; total length of specimen, 125 mm. Both specimens from Cordillera del Dué, above Río Coco, 1150 m elev., Napo, Ecuador.

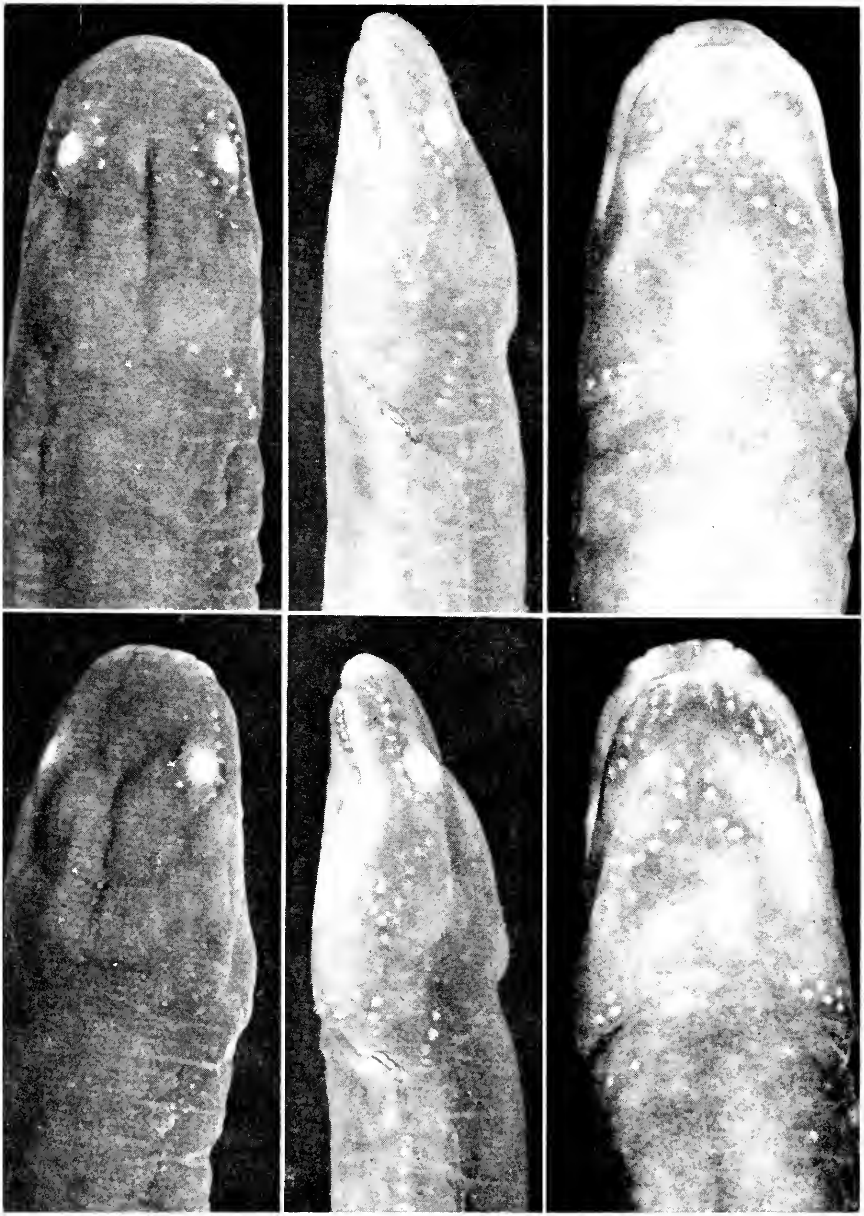

FIG. 5. *Epicrionops petersi petersi* Taylor. Larvae. Upper figures (three views of head), KUMNH No. 119400. Head width, 6 mm; total length of specimen, 135 mm. Lower figures (three views of head), KUMNH No. 119397. Head width, 6.1 mm; total length of specimen, 134 mm. Both specimens from Cordillera del Dué, above Río Coco, 1150 m elev., Napo, Ecuador.

THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. XLVIII Pages 869-949 July 2, 1970 No. 26

An Introduction to the Phytogeography of Kansas

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ABSTRACT

The vascular flora of Kansas is composed primarily of species which are not confined to the Great Plains. Most of these are believed to have migrated into the area during Tertiary or later times, though it is probable that some evolved within the Plains. Paleobotanical evidence, recorded accounts of the native flora at the time of the white man's arrival and present distribution patterns suggest that the flora of Kansas is related to eight major centers of frequency—the east, northeast, southeast, south, southwest, north, interior and Great Plains—and also contains a number of widespread species. Major patterns of distribution exhibited by species entering the state are described in this paper, and tentative conclusions regarding the ecological factors which seem to be most influential in determining these patterns are discussed. It is suggested that much more work on the biosystematics of plains species will yield information of real value in interpreting phytogeographical problems.

INTRODUCTION

Kansas has only a single species of Embryophyta, the moss *Aschisma kansanum*, which, as far as is known, is entirely confined to the state. Another moss, *Grimmia teretinervis*, collected in Scott and Norton counties, is otherwise known only from the Hudson Bay area and from the Alps. Among the angiosperms, *Oenothera fremontii* is limited to north-central Kansas and extreme south-central Nebraska. *Clematis fremontii* has a similar distribution in Kansas and Nebraska but also has a disjunct population in eastern Missouri. *Phlox oklahomensis* is known only from Woodward County, Oklahoma, and from Butler, Cowley, Elk and Chautauqua counties, Kansas. With the exception of these five species, Kansas is populated by plants which are relatively widespread and which are believed to have migrated into the area during later Tertiary and more recent times, although it is probable that some have evolved within the plains. As one studies the distributions of these migrant taxa, certain recurring patterns become obvious. For example, plants which are related to the flora of the southeastern United States tend to share a common area within the state, as do species which are characteristically northeastern. Some members of these two floras overlap in distribution, but even where they do not overlap, there are indications that some of the same ecological factors limit both elements in their westward distribution. It is the purpose of this investigation to provide a more thorough understanding of the relationships of the Kansas flora to those of other regions and, when possible, to consider those major ecological and evolutionary factors which define areas of distribution within the state. Nomenclature for the vascular plants is according to Gleason and Cronquist (1963) except for certain recent monographs and revisions.

PALEOBOTANICAL RECORDS FROM THE CRETACEOUS TO THE RECENT

The distribution of any species in a modern flora may depend in part upon past ecological conditions as well as upon present ones; thus it is pertinent to consider the paleobotanical history of central North America since the close of the Cretaceous Period. During the Cretaceous, much of the interior of the continent was covered by inland seas and the climate was warm and humid. With the uplift of portions of the Rocky Mountain system at the end of the Cretaceous, this interior region was exposed, and the land became available to terrestrial plants. By the Eocene, the Rocky Mountains were much reduced; by the Oligocene, peneplanation was complete. The Mississippi Embayment, together with moist winds from the Pacific, allowed for a rather uniform oceanic climate with summer rains and temperatures that rarely fell below freezing. During the Early Eocene, most of the eastern United States, Canada and Alaska were occupied by the Arcto-tertiary flora. Subtropical conditions extended as far north as present North Dakota, and temperate conditions reached nearly to the North Pole. Samuel Aughey (1880) records *Populus, Quercus, Salix, Ficus, Liquidambar, Sassafras* and palms from deposits in Nebraska which Chaney and Elias (1936) assign to this early Tertiary Period. MacGinitie (1962) includes *Ailanthus, Cercidiphyllum, Dipteronia, Engelhardtia* (Asiatic type), *Exbucklandia, Glyptostrobus, Idesia, Ketelleria, Koelreuteria, Metasequoia, Paliurus, Paulownia, Pterocarya, Trapa* and *Zelkova* as being characteristic of the Arcto-tertiary flora during the Oligocene and into the Miocene. He lists *Acer, Betula, Carya, Castanea, Fagus, Fraxinus, Hydrangea, Liriodendron, Nyssa, Quercus, Ulmus* and others as being characteristic of the later Miocene Arcto-tertiary flora.

The western part of the United States as well as the Gulf Coast and Florida were occupied during the early Eocene by the Neotropical-tertiary flora which was characterized by tropical and subtropical plants, especially by trees with broad, thick evergreen leaves as in the Lauraceae. According to MacGinitie, this group increased in importance until late Eocene or Oligocene and included genera such as *Cedrela, Engelhardtia, Thouinia, Meliosma* (Mexican type), *Cissampelos, Rhamnidium, Davilla, Chrysophyllum, Petrea* and *Persea.*

The Mexican Plateau was the center of origin of the Madro-tertiary flora which began perhaps as early as the Eocene "on scattered dry sites and on the lee sides of high ridges and mountains" and which consisted primarily of small trees, shrubs and grasses (Kendeigh, 1961).

Toward the end of the Oligocene, the North American climate was gradually becoming cooler, although large trees still prevailed well to the north. Beginning during the Miocene and increasing into the Pliocene (decreasing thereafter), there was extensive uplifting in the Rocky Mountains, Appalachians, Ozarks and Ouachitas. With the continuing cooling process, there was a general southward shift of the northern boundaries of temperate and tropical species. The erection of high mountains between the Pacific Ocean and the interior of the continent, together with the uplift of the Ozark region and the subsequent drainage of much of the Mississippi Embayment, produced a much less humid climate in the Great Plains region. Apparently as a result of reduced summer rainfall and decreased reliability of rainfall, many of the East Asian and East American elements had disappeared from this area by the end of the Miocene, and hardy drought-resistant plants from northern Mexico (elements of the Madro-tertiary flora) were migrating northward into the Great Plains and the western slopes of the Sierra Nevada (Chaney, 1947).

The fossil record in the Great Plains is scanty, and interpretations of the material available do not agree as to the type of vegetation which occupied this region during the late Tertiary. Chaney and Elias (1936), primarily on the basis of fossil floras and faunas from Brown County, Nebraska (Upper Miocene to Lower Pliocene); Beaver County, Oklahoma (Lower Pliocene); and Logan County, Kansas (Middle Pliocene), postulate the existence of extensive grasslands with trees limited to stream borders and lake margins. MacGinitie (1962), working with a larger but older Upper Miocene flora (Kilgore Flora) from Cherry County, Nebraska, believes the area was occupied by a "savanna type of vegetation with well-forested river bottoms and an open pine-oak forest of subhumid aspect on the interfluves," and that "the present prairie type of treeless vegetation is a product of the Pleistocene climates." Wells (1965) also states that "the extensive treeless grassland in the plains region may be a relatively recent development." It is interesting to note, however, that in contrast to the megafossil flora described by MacGinitie, which contained only trees and shrubs, the Pliocene strata of the Ogallala formation as described by Segal (1966) contain 32 grasses and 10 forbs but only one tree, *Celtis*. Modern counterparts of the fossil grasses and forbs are typical prairie species, and *Celtis* is commonly found along streams in semi-arid grassland regions. Other indications of a drier climate during the Pliocene, such as modifications in leaf structure and stratigraphical evidence of a declining water table, are discussed by Chaney and Elias (1936) and by Frye and Leonard (1957). The relative paucity of Pliocene fossils is also suggestive of a more xeric environment since fossilization is thought to occur less readily in a dry situation than in a wet one.

It is further interesting to note that of the modern species most similar to MacGinitie's 28 megafossil species, nine (according to MacGinitie) are presently associated with that flora which extends from southeastern Nebraska to the Ozarks and eastward to the Appalachians; six are now restricted to the southwestern United States and adjacent Mexico; and three occur in both of these regions. Five of the modern related species are growing now at the fossil site. Three of these, *Celtis occidentalis, Fraxinus pennsylvanica* and *Ulmus americana*, are related to eastern floras; and two, *Acer negundo* and *Ribes aureum* (including *R. odoratum*), occur in both areas.

Bessey (1887) describes an interesting modern locality approximately 35 miles east and a few miles north of the Kilgore fossil site, where a small tributary of the Niobrara River, Long Pine Creek, runs through a deep and winding canyon. Bessey refers to the country surrounding the canyon as "absolutely treeless . . . the surface in many places thrown up into rounded hills of what must have once been drifting sand." In this canyon, he found great numbers of *Pinus ponderosa* var. *scopulorum, Prunus demissa, Ribes aureum, Rhus trilobata,* and an oak approaching *Quercus undulata,* all western species, growing together with *Juglans nigra* and *Ostrya virginica,* both at the western-most limits of their ranges. Other plants growing in the canyon also indicate that the area is, as Bessey calls it, "a meeting place for two floras." Might not the Kilgore flora have been growing in just such a canyon as the one at Long Pine? The protected nature of the canyon would have allowed for the survival of more mesic species than could have existed on the surrounding upland and at the same time would have made fossilization of plant parts more likely. Although MacGinitie feels there is no definite paleobotanical evidence indicating the existence of widespread treeless prairies or steppes in the Tertiary, we have been unable to discover any data which would unquestionably exclude the existence of a type of vegetation such as that postulated by Chaney and Elias.

During the Pleistocene, the North American climate became more humid. The cooling trend which had begun in the Oligocene culminated in four major periods of glaciation which alternated with inter-glacial stages thought to have been as warm, or nearly so, as the present (Polunin, 1960). Only the first two major advances—the Nebraskan and the Kansan—reached into Kansas, and these entered only the northeastern corner of the state. The Wisconsin glaciation, being the latest and covering much of the same area as the previous three, is the most important when one is considering modern distribution patterns. At its maximum, approximately 18,000 years BP or even later, the Wisconsin glacier reached into southeastern South Dakota, extended northwestward toward North Dakota, roughly paralleling the present course of the Missouri, and east-southeastward across northern Iowa (Jones, 1964).

During the glacial advances, some species of plants and animals were forced to exist southward, while others were eliminated completely. Workers do not agree upon the distance south of the glacial boundary to which the effects of the ice masses were felt. According to Braun (1928), the arctic and coniferous belts intervening between the ice and the more southern deciduous forest probably were not wide, "for the effects of glacial refrigeration do not seem to have extended far beyond the limits of the ice cap." Deevey (1949) feels, however, that "glacial chilling in the southeastern states must have been fairly extensive and that the warmth-loving species, including many or perhaps most of the 'Miocene relicts,' survived in peninsular Florida and in Mexico, and have subsequently migrated to their present localities." The effects of Pleistocene glaciation upon speciation, particularly in regard to isolation of populations, creation of new habitats, hybridization and polyploidy, have been discussed in some detail by Anderson (1949), Stebbins (1950), Braun (1955) and others.

Pleistocene fossils from the Great Plains are primarily limited to pollen and other materials from bogs and marshes. Horr (1955) discusses a pollen profile from Muscotah Marsh in Atchison County, Kansas. The material, according to Horr's interpretation, gives evidence of a trend from a cool, moist climate (*Abies* dominant, with *Tsuga, Picea* and *Larix*) to a warmer, drier climate (decrease in coniferous pollen accompanied by an increase in *Corylus, Populus* and *Quercus*) followed by a reversal to a cool, moist climate with coniferous vegetation. The remaining layers of the marsh indicate the development of a grassland association, dominated by Cyperaceae, Chenopodiaceae and Gramineae, probably brought about by a continuing decrease in moisture and an increase in temperature. McGregor (1968) gives a C-14 date of 15,500 years BP ± 1,500 for *Abies* needles obtained from the bottom layer of a core from the same marsh. This would seem to coincide with the Cary Substage of the Wisconsin glaciation at which time a lobe of the glacier reached into north-central Iowa (Wright and Ruhe, 1965). Evidently the climate approximately 200 miles southwest of the glacial margin was cool enough to permit the growth of a boreal type of forest. According to McGregor, "it would appear that the transition from boreal forest to prairie began about 11,000 BP and was completed about 7,000 BP. Between 7,000 and 4,000 BP the present vegetation of the area of northeast Kansas was reached." These dates agree with those given by Wright (1968) for Illinois and the general area of the Prairie Peninsula.

During the Late Pleistocene, the Great Plains is thought to have experienced a warm, wet period usually referred to as the early Hypsithermal Interval. Jones (1964) imagines a "westward extension far onto the plains of elements of the eastern deciduous forest and probably also tallgrass prairie—forest species along the river systems and on favored drier sites, and tall grasses on the uplands" during this time. Disjunct populations of two species of woodland mammals, *Peromyscus leucopus,* the white-footed mouse, and *Neotoma floridana,* the wood rat, support this theory. Distribution patterns of various plants, including the species mentioned in Bessey's paper of 1887, also uphold this theory. Rydberg (1896) years ago noted the similarity between the flora of the Black Hills and that of the Great Lakes region. Watts and Wright (1966) also discuss western and eastern species which occur in the Black Hills and state that conifers from Canada and from the eastern Rockies probably were in contact in the western Great Plains during the Wisconsin and that they probably provided a forest "bridge" by which exchange of species between the two types of forest was possible.

As the Pleistocene drew to a close, the climate became progressively drier and warmer. A period (or perhaps several periods) of frequent, widespread and prolonged drought conditions, the later Hypsithermal Interval, allowed for an eastward extension of the central grasslands through the lower Great Lakes region perhaps as far east as the Mohawk Valley, New York. Borchert (1950) presents a brief and lucid account of events as they are thought to have occurred during this time. Briefly they are as follows. As the continental glaciers retreated northward, the boreal spruce forests followed. These were not replaced immediately by the birch-beech-maple-hemlock association which is presently situated between the boreal forests and the more southern deciduous forests. In the northeastern United States, the area vacated by the boreal forests was occupied first by a wedge of oak forests, indicating relatively drier conditions, and then, for a longer period, by grasslands. Schmidt (1938) and Smith (1957) present zoogeographical evidence which substantiates this theory of an eastward extension of the prairie peninsula. Davis (1965) maintains that New England may not have felt the effects of the late Hypsithermal Interval but that enough information to reach a conclusion is not yet available. Wright (1968) synthesizes much of the most recent data regarding the history of the Prairie Peninsula. In the interior plains region, the spruce forests were replaced immediately by a grassland type of vegetation.

After the drier late Hypsithermal Interval, as conditions became cooler, the grassland peninsula was invaded by the deciduous forests, leaving remnants of the prairie stranded in Iowa, Illinois, Indiana, Ohio, Pennsylvania and New York. During the driest parts of the Hypsithermal Interval, the flora of eastern Kansas would have included fewer mesic species than it does now, but the present flora certainly was established long before white men arrived in the New World.

RECORDED HISTORY OF THE INTERIOR GRASSLANDS

Kansas is situated in a region variously referred to as the Great Plains, the Prairies and Plains, the Central Grasslands or the Interior Plains. Eastern botanists, ecologists and geographers writing about the region which extends from North Dakota to central Texas and from the eastern base of the Rocky Mountains to the edge of the eastern deciduous forests have tended to treat it as a rather homogeneous area consisting of vast expanses of monotonous grassland fringed on the east by remnants or invaders from the eastern forests. The names applied to these central states reflect this trend in thought. In vegetational and climatic descriptions, the gradual increase in elevation and gradual decrease in rainfall from east to west are usually emphasized, while physiographic regions and north-south changes in length of growing season and average temperature (as well as the floristic changes that accompany them) often go unmentioned. A reader unfamiliar with the central states could easily fall (and many do) into the habit of regarding the region as a flat to rolling grassland differing from place to place only in the height or sparseness of its plant cover and in the amounts of its meager rainfall.

This traditional notion of homogeneity and barrenness was continuous from the 16th century until the end of the 19th century and still has not been completely dispelled. This seems to be based upon the history of the region as much as upon its physiography or flora. It is furthered by the fact that major highway systems in the plains states run east and west—parallel to the drainage patterns—thus affording much less variation in relief and vegetation than one would observe if traveling from north to south. The role of the history of the region in painting an image of barrenness and monotony in the central prairie and plains states is evident in the following summary. Those interested in a more detailed account are referred to Baughman (1961), Miller, Langsdorf and Richmond (1961) and Wedel (1959).

Spanish conquistadores who in 1541 came as far as Rice County, Kansas, in their search for Quivera were among the first white men to leave a written description of that part of the state. "The country is like a bowl," they declared, "so that when a man sits down, the horizon surrounds him at the distance of a musket shot" (Farb, 1964). Had they accidently found their way to the Chautauqua Hills in southeastern Kansas, their impression might have been much different.

After Louis Jolliet and Jacques Marquette traveled down the Mississippi River in 1673, the French began to explore the Missouri River as a possible route to California. French explorers produced some maps—the first in fact which made reference to the Kansa Indians for which the state of Kansas was named—but left very little in the way of written descriptions of the land or its plants.

Few Anglo-Americans other than traders and trappers reached the central states until the early 1800's. The acquisition of the Louisiana Territory in 1803 prompted the government to sponsor exploratory expeditions such as those led by Lewis and Clark, 1803-1806, and Pike, 1806. Lewis and Clark spoke disparagingly of the northern grasslands, and Pike, who explored the grasslands of Nebraska and Kansas in the fall of 1806, was also left with a poor opinion. He called the Great Plains "a desert—a barrier—placed by Providence to keep the American people from a thin diffusion and ruin" (Jackson, 1966). In 1819, Major Stephen Long led another group into the area. It was on his map, according to Miller, *et al.* (1961), that the High Plains or short grass prairie was first labeled the "Great American Desert." Forty years later, describing for the readers of the New York *Tribune* his overland journey to Colorado and California, Horace Greeley was still proliferating the myth of the "American Desert . . . the acme of barrenness and desolation" (Caldwell, 1940). As James Malin (1967) points out, "this desert tradition was so firmly embedded in the public mind that it became an obstacle to thinking about the area, and has today been eradicated only in part."

Academic activities during the first decade of the 19th century were primarily confined to the eastern seaboard—to cities such as Boston and Philadelphia. There were, however, a handful of naturalists already contributing to the inventory of the plants of North America. Among these was a young English naturalist, Thomas Nuttall, who was the first person to bring back significant observations and materials relating to the flora of the central United States. During 1810-11, he traveled into what is now Nebraska and the Dakotas (Graustein, 1967) and in 1818-20 he traveled westward across Arkansas and into eastern Oklahoma. His longest trip (1834-36) began at Independence, Missouri, and continued up the Missouri and Kansas rivers, north to the Platte River, up the North Fork of the Platte and across the Rocky Mountains. From these expeditions Nuttall brought back many previously undescribed plants. A study of Gates' *Flora of Kansas* (1940) shows that of the 1,626 native taxa listed, 164 of them or about 10% were first described by Nuttall. Another 11 species were named after him (e.g., *Zygadenus nuttallii*, *Viola nuttallii*, *Sedum nuttallianum*). A remarkable record for one person!

As more people began to move west, two major highways were responsible for the founding of trading posts and primitive settlements to serve travelers. The Santa Fe Trail, first used by wagon traffic in 1822, was used primarily for trade with the Spanish Southwest. The Oregon Trail, especially important during the late 1830's to 1850's, was, however, primarily a road of emigration (Miller, *et al.*, 1961). Little botanizing took place during the years of active settlement, but journals of travelers and settlers provide some descriptions of the native flora at that time. Many of the settlers moving west looked at the plains somewhat as Pike did; they felt it was a barrier to be crossed before their destination farther west could be reached. It is interesting to note, however, the difference in comments made by travelers who crossed through the grasslands in the spring and early summer and those who came through in late summer and fall as Zebulon Pike did. Heinrich Möllhausen, who traveled the Santa Fe Trail from Santa Fe to Leavenworth in 1858, passed through Morton County, in the southwestern corner of Kansas, in late June. He speaks of water shortages and hot weather, but just as frequently describes green, grassy valleys and violent thunderstorms.

In 1842, Frémont led a mapping expedition across the plains to the Rocky Mountains, following the Oregon Trail to the forks of the Platte and continuing as far west as the Wind River Mountains of Wyoming. They returned along the Platte and Missouri rivers. The expedition of 1843-44, according to Frémont's journal, left from "the little town of Kansas, on the Missouri frontier, near the junction of the Kansas River with the Missouri River." The route followed on this expedition was more southern than that of the previous year, following the valley of the Kansas River. They then continued west to the head of the Arkansas River and then north and west to Oregon and California. On the return journey, they crossed the Rockies near the headwaters of the Arkansas River and followed the Arkansas and Smoky Hill river valleys back to Independence. The original report of the expeditions of 1842 and 1843-44 (published by Gales and Seaton, Printers, Washington, 1845) includes a catalogue of plants collected by Frémont, with a preface by John Torrey and an appendix containing the latter's descriptions of four new genera and 13 new species collected during the second expedition.

Frémont's journal contains frequent references to species in particular and to the aspect of the vegetation in general. His daily records of latitude and longitude make it possible to determine with reasonable accuracy his location at any given time and to compare his observations of flora and soils with present knowledge of them. For example, on the morning of June 16, 1843, Frémont's party was approximately 265 miles west of the mouth of the Kansas River (in the vicinity of present Lucas). An entry in his journal pertaining to that day's travel reads as follows: "After a few hours' travel over somewhat broken ground, we entered upon an extensive and high level prairie, on which we camped toward evening at a little stream, where a single dry cottonwood afforded the necessary fuel for starting supper. Among a variety of grasses which today made their first appearance, I noticed bunch grass *(festuca)*, and buffalo grass *(seslaria dactyloides)*. *Amorpha canescens* (lead plant) continued to be the characteristic plant of the country, and a narrow-leaved *lathyrus* occurred frequently, with a *psoralia* near *psoralia floribunda*, and a number of plants not hitherto met, just verging into bloom." Frémont and his group had that day emerged from the Dakota sandstone area of north-central Kansas and entered the High Plains of short-grass prairie region. All of the plants he describes above are presently known to occur in the same area.

The journals of these expeditions, diaries and letters of early settlers, and other historical documents are an aid to determining the native flora of the central states at the time of the white man's arrival. Since the original landscape has by now been largely destroyed by cultivation, over-grazing and other activities connected with human habitation, these records can be of value to a person studying natural vegetation areas in general or distribution of species in particular. Such documents must be used with a bit of caution, however. Most of the early settlers had no formal training in natural history and their identification of plants may not always have been correct. Common names also pose a problem, as they may not always apply to the same plant in different parts of the country. One must also bear in mind certain prejudices that the settlers brought with them. To lumbermen or to people who had just traveled many miles through forests, a region which was relatively treeless seemed barren and unprofitable. This "forest-mindedness" of the easterners was one of the most powerful factors in establishing the "Great American Desert" myth mentioned previously. Another point is made by Braun (*in* Steyermark, 1959) who warns that "the unusual was often emphasized," in these old accounts. At the same time, the usual was often neglected. The following quotation from Möllhausen's 1858 journal (see Möllhausen, 1948) illustrates this point well: "On July 5, we continued our trip along the river valley; the road was good, the weather extremely pleasant, but there was so little change in the scenery that it could be considered as non-existent. When we therefore observed indistinct forms of three or four cottonwood trees on the far horizon or went past islands on which willows grew, we turned our full attention to them, and found objects beautiful and pleasant which would have gone unnoticed in other regions."

In 1856 the southern boundary of Kansas was surveyed. Several accounts of the surveying expedition are available and all include frequent references to the flora, soils, topography and wildlife of the areas through which the party traveled. Sufficient landmarks are given in these reports to permit comparison of the vegetation with that of the present. It is easy to recognize the Chautauqua Hills, for example, which are described as country "with a broken and irregular appearance . . . many ridges very rocky and covered with a dense growth of black jack." West of the Chautauqua Hills, the surveying party left the "timbered country" and moved into prairie. "The dividing ridge . . . a plateau about 300 feet above the valley" is the eastern escarpment of the Flint Hills. The plateau is described as having "sides very abrupt and rocky" with "limestone near the summit" (Miller, 1932).

In addition to organizing the territories of Kansas and Nebraska, the bill of 1854 also repealed the Missouri Compromise of 1820 and during the era of violence which resulted, little botanizing was done in Kansas. In spite of this political unrest, some academic progress was made during the 1860's. In 1863, the Kansas State Agricultural College (now Kansas State University) was established at Manhattan, and Lawrence was chosen as the site of the University of Kansas. F. H. Snow, one of the first three faculty members at the University, and his students assembled the first nucleus of an herbarium. In 1867, "moved by the impulses of the age," 17 Kansas naturalists founded the Kansas Natural History Society which, in 1871, became the Kansas Academy of Science (Parker, 1872). Many of the papers dealing with the Kansas flora have been published in the *Transactions* of this academy.

In the 1870's, serious work on the flora of Kansas began and check lists were prepared. From 1872 to 1884, Reverend James H. Carruth, a staff member at the University of Kansas, devoted full time to the study of the state flora. Carruth (1877) published his *Centennial Catalogue of the Plants of Kansas* in which he included 1,082 plants and indicated that 40 were introduced and 142 not known east of the Mississippi. For the first time, specimens were kept in Kansas rather than sent east or to Europe. Ministers, physicians, teachers and others sent from a few to over 500 specimens to Carruth for his study. A series of papers reporting additions to the state's flora resulted. In 1883, Carruth reported that "the additions now made are but few. The field has been reaped and henceforth I can only give the gleanings." Carruth's last paper (1885) brought the check list of Kansas plants to 1,515, and he stated that "the work of making a catalogue of the plants of Kansas is so nearly completed, and my salary as a state officer is so very meager, that I have done but little myself." Just prior to this, Carruth's disagreements with Snow over Darwinism had precluded further work by Carruth. Unfortunately, none of Carruth's collections are present at the University of Kansas and their disposition is unknown.

Carruth's anti-Darwinism did not deter others from floristic studies and field work. Individuals from over the state began contributing articles on the flora. Plank (1883) published *A Preliminary Notice of the Flora of Montgomery County, Kansas* and Scribner (1885) produced *A Contribution to the Flora of Kansas: Gramineae* in which he stated "probably only half of the grasses in Kansas are known."

During the 1880's, M. A. Carleton and W. A. Kellerman established the Kansas State Herbarium at Kansas State University. During the 1890's, A. S. Hitchcock developed a remarkable field program aimed at obtaining a complete collection of plants from each county of the state. By 1900 a minimum of 100 species had been obtained from each of the 105 counties. These collections were the basis of Hitchcock's (1899) *Flora of Kansas Maps* which consisted of a series of dot maps giving the distribution of flowering plants by counties.

Upon the transfer of Hitchcock to the National Herbarium in Washington, D.C., B. B. Smyth, curator of the State Museum of Natural History in Topeka, continued further work on the state's flora. Many individuals sent material to him and he published a series of lists of Kansas plants. In 1900, he published his *Plants and Flowers of Kansas* as his fourth contribution. He planned a fifth and complete list but lived to complete only a third of the task which was published in 1912. Smyth's herbarium contained over 4,000 specimens and bundles of unlabeled material. In 1926, it was given to Kansas State University. Unfortunately, specimen evidence for many of his Kansas reports was not present in his collections.

In the period of 1908-1912, Professor F. U. G. Agrelius was employed during the summers by the University of Kansas to collect plants in the northern and western areas of Kansas. His collections, containing many new state records, formed the basis of the University Herbarium. Agrelius also salvaged the collections of F. H. Snow, his students and other donors and put the herbarium in order.

In 1919, F. C. Gates joined the staff at Kansas State University at Manhattan and, though trained as an ecologist, became the most productive worker on the state's flora until his death in 1955. During his tenure, nearly 25,000 specimens of Kansas plants were added to the herbarium. Using the material gathered earlier through the efforts of Hitchcock, he was able to produce a series of handbooks on plants of Kansas. His most important contribution was his *Flora of Kansas* published in 1940. This work for the first time included a carefully prepared annotated list of all Kansas vascular plants, as well as maps giving distribution of each species by counties. He continued publishing notes, additions and corrections until his death.

In the period from 1933 to 1954, Professor W. H. Horr at the University of Kansas conducted fieldwork over much of Kansas and by 1954 had accumulated additions to the University Herbarium totaling several thousand sheets. He was assisted in the latter phases of the work by R. L. McGregor who took over the operation in 1954. By 1968, the Kansas specimens in the University Herbarium numbered over 75,000.

Throughout the history of study of the state's flora, the emphasis has been on completing the inventory and much work still remains to be done. Basic and applied ecological studies have been made on prairies and range lands. Very little has been written, however, on the relationship of the Kansas flora to that of other areas. Hitchcock (1892) published a short paper on *The Relations of the Composite Flora of Kansas*. Of 47 genera studied, Hitchcock related 31 to the Mexican flora; 28 to the southeast; 23 to the northeast; and eight to the Rocky Mountain flora. He includes 40 of these in two to three different floras. Fearing (1952), briefly alludes to regional affinities of the Kansas flora but does not consider the matter in depth. McGregor (1955) states that in the Hepaticae "a relationship to the southern, southeastern and southwestern hepatic floras is evident." He lists only one species which would indicate a relationship to northern floras. According to Smith (1966), only one of the moss species characteristic of the western two-thirds of the state is eastern in distribution, and this single species is abundant only in the Blue Hills physiographic area. Smith states that "from east to west in the Great Plains there is a decrease in the percentage of mosses of widespread distribution and an increase in the percentage of mosses of western affinities" until, in the High Plains area, 60% of the characteristic species are related to western floras and 40% are of widespread distribution. Lathrop (1958) presents a carefully prepared study of the flora and ecology of the Chautauqua Hills in southeastern Kansas. His data indicate that the flora of that region is influenced primarily by elements of the Texas Biotic Province to the south but also contains elements from the eastern and southeastern United States.

METHODS USED IN THIS STUDY

Gates (1940) included 1,872 species in his check list of Kansas plants. Of these, 779 have not been considered for various reasons: 326 are introduced, 177 are known from a single collection only, and another 175 are too poorly known to be considered in a study of distribution patterns. An additional 101 species have been deleted because of nomenclatural changes, monographs, revisions and other studies. On the other hand, 108 new species have been added to the list since 1940, bringing the number of species which would be useful in a survey of distribution patterns to a total of 1,201. For this study, 479 well-collected vascular species native to Kansas were selected as having sufficient data available concerning them, and their distributions in the central states area were mapped by counties. Distribution data were obtained from the herbaria at the University of Kansas, Kansas State University, the University of Nebraska, the University of Oklahoma and Oklahoma State University. For distributions in Missouri, the detailed maps in Steyermark's (1963) *Flora of Missouri* were used. This information was supplemented by our own field studies and by general statements of distribution as given in manuals, monographs and other literature. The species included in this investigation represent 15 pteridophyte genera and 250 angiosperm genera from 85 families.

Once the species were mapped, they were sorted into groups according to their present centers of frequency within the United States. All plants considered fell into one of nine groups: eastern, northeastern, southeastern, southern, southwestern, northern, interior, Great Plains or widespread. These groups are defined in the section on geographical affinities of the Kansas flora. Once sorted into these categories, the species were further subdivided according to the minor patterns or "sub-patterns" which they displayed within the major patterns. In the final stages of the investigation, an effort was made to correlate these patterns and sub-patterns with past and present ecological conditions.

PROBLEMS ENCOUNTERED

In a study of this type which depends heavily upon the research and collections of previous workers, there are a number of inevitable problems, particularly in regard to determining the center of frequency of any given species. When transferring dots from maps in manuals and monographs, it is impossible to tell whether one dot represents hundreds of native plants or a single introduced specimen collected in a freight yard. Statements of distribution as given in manuals are usually very general and do not accurately indicate a plant's distribution or center of frequency. Remarks on herbarium labels are quite helpful, but all too frequently information concerning abundance or general distribution is found wanting. Dot maps also tend to reflect areas of collecting (or lack of it) and number of specimens examined. We have relied upon our experience in the field to at least partially solve this problem.

Species which involve taxonomic problems also present difficulties. Should *Monarda fistulosa*, for example, be mapped as one species ranging from southwestern Quebec and western New England, south to Maryland, upland Georgia, and west to British Columbia and Arizona? Or should it be mapped as two species, *Monarda fistulosa* with an eastern distribution and *Monarda menthaefolia* with a western distribution? In cases such as this one, we followed the most recent and most comprehensive treatment of the genus available. In many groups, of course, the taxonomic problems have not been solved; in fact, it appears that many are as yet unrecognized. As a matter of convenience, these species or species complexes were eliminated from this study.

A third problem arises when one begins to sort maps into groups of like distribution patterns. All of the plants whose center of frequency is in the northeastern United States do not have exactly the same area of distribution, nor do the plants from the southwest, or from any other area. Within any one group, there is a species with a "minimum area of distribution" and another with a "maximum area of distribution," so to speak; the remaining species show a continuous gradation from one extreme to the other. This can be seen in Figure 1 which shows both the general range of southwestern species as defined in this paper and the individual areas of distribution of several species within the group. There is also a continuous gradation between any two adjacent centers of frequency. Some species are clearly confined to the northeastern United States, while others clearly occur throughout the eastern half of the country. However, there are other species which, while occurring south of the boundary between the northeast (*Gray's Manual* range) and the southeast (*Small's Manual* range), do not extend southward to the Gulf States. Into which series should these species be placed? The same situation arises when one attempts to determine whether a plant is primarily southeastern or southern in distribution or whether another is southern or southwestern. In the case of each individual species, a decision was made based upon frequency of occurrence at the margin of its range.

GEOGRAPHICAL AFFINITIES OF THE KANSAS FLORA

Eastern Species

Of the 479 species studied, 169 or one-third occur throughout the eastern half of the United States and typically range from Maine to Florida, west to Minnesota and Texas (Fig. 2). Fifty-nine of these are woody plants. According to their habitats, the eastern species can be broadly categorized as elements of the forest, forest border and open areas, stream banks and marshes, tallgrass prairie, or sandy open areas and gravelly hillsides (see Table 1). Species which are most common in forested areas include

Table 1. Habitat preferences of eastern species.

Habitat	No. species
1. Forest	64
2. Forest border and open areas	37
3. Stream banks and marshes	27
4. Tallgrass prairie	26
5. Disturbed areas, sandy open places and gravelly hillsides	6
6. Occur in both (2) and (3) or in (3) and (4)	9
	169

Asplenium platyneuron, Cornus florida, Hystrix patula, Osmorhiza longistylis, Ostrya virginiana, Podophyllum peltatum, Quercus stellata, Sanguinaria canadensis and *Vaccinium stamineum*. Species usually associated with forest borders or open areas include *Clematis virginiana, Corylus americana, Euonymous atropurpureus, Panicum sphaerocarpon, Phytolacca americana, Quercus prinoides, Sassafras albidum* and *Silene stellata,* while *Anemone virginiana, Betula nigra, Carex frankii, Onoclea sensibilis* and *Salix caroliniana* occur primarily along stream banks and in marshy areas. Tallgrass prairie species include *Camassia scilloides, Castilleja coccinea, Eryngium yuccifolium, Hypoxis hirsuta* and *Penstemon digitalis.* Species such as *Aristida oligantha, Helianthus mollis* and *Rhus copallina* are usually found in disturbed areas, sandy open places and on gravelly hillsides, while *Carex cephalophora, C. granularis* and *Juncus biflorus* may occur in moist areas along forest borders, stream banks and marshes or moist grasslands.

When one considers the distributions of these eastern species within Kansas and within the Great Plains as a whole, five types of patterns become immediately obvious. The first is displayed by *Carex rosea* and *Orchis spectabilis* which are representative of a small group of plants that reach their westernmost limits of distribution in northeastern Kansas. Both are forest species and are rarely collected.

A second small group of eight species extends a short distance into the northeastern and southeastern corners of the state but not into east-central Kansas. These eight—*Amelanchier arborea* (Fig. 3), *Anemonella thalictroides, Cubelium concolor, Dicentra cucullaria* (Fig. 4), *Helianthemum bicknellii, Quercus imbricaria, Sanguinaria canadensis,* and *Uvularia grandiflora*—occur primarily in forests or forest border situations and tend to skirt the arm of tallgrass prairie which extends eastward from the Flint Hills through Coffey, Anderson and Linn counties, Kansas, into Bates County, Missouri.

Forty-one species, approximately one-fourth of the eastern species studied, are limited to the southeastern corner of the state (Fig. 5). Seven of these —*Alnus serrulata, Ascyrum hypericoides, Botrychium dissectum* var. *dissectum, Cornus florida, Gillenia stipulata, Pontederia cordata* and *Vaccinium stamineum*—occur in Cherokee County only, where they are accommodated by a small area (approximately 20 square miles) of Ozarkian topography with oak-wooded hills and cherty soils. The remaining 33 are more widespread, with some distributed westward into the Chautauqua Hills and into the southern tip of the Flint Hills in Cowley County.

A fourth type of pattern is displayed by a group of 74 species whose western-most boundaries are roughly north-south lines within Kansas. In Nebraska and the northern Great Plains some of these tend to extend as much as 150 miles farther west than in Kansas. Some species such as

Carex retroflexa, Rosa carolina, Cystopteris protrusa and *Crataegus crus-galli* reach only into eastern Kansas, while others such as *Populus deltoides, Gleditsia triacanthos* and *Celtis tenuifolia* cross the entire state. Most fall somewhere in between these two extremes. Westward across Kansas, the number of eastern species present gradually decreases, as does the number of individuals within any one species. Within this particular pattern, there are two minor sub-patterns. Some plants, particularly those of forest, forest border or stream bank, tend to move westward along river systems, producing an effect of feathering or dove-tailing. Others have their westward dispersal abruptly curtailed. In the case of *Podophyllum peltatum, Quercus marilandica, Q. velutina, Rosa setigera* and others, this limitation seems to correspond with the eastern edge of the Flint Hills, while with species such as *Aristida oligantha* and *Parthenocissis quinquefolia* it seems to parallel the eastern edge of the High Plains. It should be emphasized, however, that it is impossible to find any *single* factor which limits all or even a large number of these eastern species in their westward distribution. They simply do not march as a group to some one barrier and then stop. Instead, there is a gradual reduction in the number of species and of individuals from east to west as those less able to withstand the habitats of central and western Kansas drop out.

The fifth pattern displayed by the eastern species is one of a great arc northward and westward around the southern half of the Great Plains, sometimes extending southward again in the Rocky Mountains (Fig. 6). In Nebraska, the southern boundary of this arc approximates the southern extent of glaciation. Of the 44 species which exhibit this pattern, only 29 have a continuous distribution across the plains. These include *Mimulus ringens, Impatiens capensis, Carex blanda, Hypoxis hirsuta, Bromus purgans* and *Smilax herbacea.* Within Kansas, they extend westward various distances. The remaining 15 extend westward into eastern Kansas and Nebraska and sometimes into eastern North and South Dakota and then have disjunct populations in the canyons of the Niobrara River in north-central Nebraska, in the Black Hills of South Dakota and/or in the Rocky Mountains, suggesting that at one time they also had a continuous distribution across the plains. The more mesic climate of the early Hypsithermal Interval could have allowed these species to migrate westward along the river systems or perhaps across the uplands as well. The drier climate of the later Hypsithermal Interval and of Recent times apparently eradicated many suitable habitats in the plains area and left relict populations stranded in the regions already mentioned. Species in this group include *Anemone virginiana* (Fig. 7), *Aquilegia canadensis* (Fig. 8), *Arisaema triphyllum, Corylus americana, Hystrix patula, Osmorhiza longistylis* (Fig. 9) and *Quercus muhlenbergii.*

NORTHEASTERN SPECIES

A second major pattern of distribution is exhibited by a group of 32 species whose present center of frequency is in the northeastern United States. Plants in this group typically range from Maine and southeastern Ontario west to eastern North Dakota and south to Virginia, Kentucky, Missouri and eastern Kansas (Fig. 10). The habitats most frequently occupied by these northeastern species are upland forest; forest border and open or disturbed situations; lowland forest; tallgrass prairies, hillsides and thickets; and aquatic habitats (see Table 2). Upland forest species include *Acer saccharum, Celtis occidentalis, Hydrophyllum appendiculatum, Quercus borealis* var. *maxima,* and *Viola sororia. Rubus allegheniensis* and *R. flagellaris* are found in forest borders and open or disturbed areas, while *Carex hitchcockiana* and *Quercus palustris* occur in lowland forests. Species which occur primarily in tallgrass prairies, on hillsides and in thickets include *Rosa blanda, Ceanothus ovatus* and *Sporobolus heterolepis.* A representative aquatic species is *Potamogeton obtusifolius.*

TABLE 2. Habitat preferences of northeastern species.

Habitat	No. species
1. Upland forest	14
2. Forest border and open or disturbed areas	2
3. Lowland forest	7
4. Tallgrass prairie, hillsides and thickets	8
5. Aquatic	1
	32

Within Kansas, the northeastern species can be divided into three minor patterns or sub-patterns. Six species—*Carex hirtifolia, C. hitchcockiana, C. cristatella, C. sparganioides, Hydrophyllum appendiculatum* (Fig. 11) and *Rosa blanda* (Fig. 12)—are restricted to the northeastern corner of the state. Three species—*Carex squarrosa* (Fig. 13), *Physocarpus opulifolius* (Fig. 16), and *Vaccinium vacillans* (Fig. 14)—occur only in southeastern Kansas although they are found throughout much of Missouri. Most of the remaining 22 occur within the eastern third of Kansas. Examples include *Quercus palustris, Rubus allegheniensis, Carex jamesii* and *Viola sororia.* Except for *Parthenocissus vitacea, Ceanothus herbaceous* and *Celtis occidentalis,* species displaying this sub-pattern do not extend westward much beyond the Flint Hills.

In all of the minor groups just discussed, there are some species which have the same tendency to arc northward and westward in Nebraska as do some of the eastern species described in the previous section of this paper. Examples include *Carex crawei, C. normalis, C. bicknellii, Sporobolus* *heterolepis, Parthenocissus vitacea, Ceanothus herbaceous* and *Tilia americana* (Fig. 15). *Physocarpus opulifolius* (Fig. 16), restricted within the state to Cherokee and Neosho counties in the southeast corner, has disjunct populations in north-central Nebraska, the Black Hills and the Rocky Mountains of Wyoming and Colorado. *Liparis loeselii*, of the north and east has been collected in Shannon County, Missouri, Pottawatomie County, Kansas, and north-central Nebraska. It is described by Steyermark (1963) as "another one of the isolated relict survivors which has been stranded in the swampy meadows . . . following one of the advances and retreats of an ice sheet during Pleistocene times."

SOUTHEASTERN SPECIES

Thirty-five of the 479 species studied occur primarily in the southeastern United States and typically range from Florida west to Texas, north to Virginia, Kentucky, Missouri and eastern Kansas (Fig. 17). This area includes the southern half of the Appalachian Upland and the Ozarkian Plateau which Fernald (1931) describes as the oldest large section in eastern North America which has been available for occupation by flowering plants. Adams (1902) and Deevey (1949) discuss the southeastern United States as a Pleistocene refugium and a center of geographical distribution of flora and fauna.

The general types of habitats in which these species are found are as follows: forest; forest border and open areas; tallgrass prairie and rocky hillsides; and streambanks and marshes (see Table 3). Examples of forest species are *Carya illinoensis, Celtis laevigata, Hexalectris spicata, Ilex decidua, Phoradendron flavescens* and *Vaccinium arboreum*. Plants usually found in forest borders or disturbed and open areas include *Ampelopsis cordata, Calycocarpum lyoni, Crategus viridis, Passiflora incarnata* and *Verbesina virginica. Bumelia lanuginosa* and *Nothoscordum bivalve* usually occur on hillsides or in tallgrass prairie, while *Cyperus densicaespitosus, Dicliptera brachiata* and *Hibiscus lasiocarpus* are found along streambanks and marshes.

Within Kansas and the Great Plains, the southeastern species display only a single major distribution pattern. All but a few, such as *Sesbania exaltata,*

TABLE 3. Habitat preferences of southeastern species.

Habitat	No. species
1. Forest	10
2. Forest border and open or disturbed areas	8
3. Tallgrass prairies and rocky hillsides	5
4. Stream banks and marshes	12
	35

Juncus validus and *J. scirpoides* which occur sporadically in Kansas and Missouri, arc across the southeastern corner of Kansas (Fig. 18). Some species—*Ulmus alata, Vaccinium arboreum, Calycocarpon lyoni* and *Hibiscus lasiocarpus,* for example—occur only in Cherokee County, while others such as *Nothoscordum bivalve* and *Ampelopsis cordata* occur as far west as Barber and Kiowa counties, Kansas. The northwestern limits of most of the southeastern species lie somewhere between these two extremes.

SOUTHERN SPECIES

Of the species studied, 42 have a center of frequency south of Kansas. The general area of their distribution is from Texas and northeastern Mexico north to Oklahoma and Kansas (Fig. 19), although some have a broader distribution extending west to Arizona, east to Florida and north to Virginia, Ohio and Indiana. Only three woody species—*Cephalanthus occidentalis, Sapindus drummondii* and *Prunus mexicana*—are included in this group. The southern species tend to occur mainly in the following type of habitats: midgrass prairie hillsides and canyons; tallgrass prairie and rocky banks; sandy tallgrass prairie; and streambanks, marshes and moist ditches (see Table 4). Plants which occur on midgrass prairie hillsides and in canyons include *Androstephium coeruleum, Echinacea angustifolia* var. *angustifolia, Sapindus drummondii, Nama stevensii* and *Oenothera oklahomensis.* The latter two are particularly common in the red gypsiferous soils of Clark, Comanche, Barber and Harper counties, Kansas, and of western Oklahoma and Texas. *Aster sericeus, Acacia angustissima, Callirhoe involucrata, Desmanthus illinoensis, Eryngium leavenworthii, Echinacea atrorubens, Penstemon cobaea, Nemastylis geminiflora, Sporobolus pyramidatus* and *Tradescantia tharpii* are species frequently found in tallgrass prairie and on rocky banks. Species of sandy tallgrass prairie include the following: *Berlandiera texana, Cleomella angustifolia, Croton glandulosus, Gaillardia fastigiata, G. suavis, Liatris squarrosa* var. *glabrata, Monarda citriodora* and *Prunus mexicana.* Plants usually found along streambanks, in marshes or moist ditches include *Cephalanthus occidentalis, Eleocharis montevidensis, Carex fissa, Marsilea mucronata,* and *Heteranthera reniformis.*

TABLE 4. Habitat preferences of southern species.

Habitat	No. species
1. Midgrass prairie hillsides and canyons	5
2. Tallgrass prairie and rocky banks	19
3. Sandy tallgrass prairie	12
4. Streambanks, marshes and moist ditches	6
	42

Within Kansas and the Great Plains, four sub-patterns of distribution are apparent. There is, however, a great deal of variation within each of these sub-patterns and much overlap among them. A group of six species—*Androstephium coeruleum* (Fig. 20), *Gaillardia fastigata, G. suavis* (Fig. 21), *Sporobolus pyramidatus, Nama stevensii* and *Oenothera oklahomensis*—come into southwestern or south-central Kansas and do not occur north of Kansas. *Cleomella angustifolia* (Fig. 22) has a similar distribution but also has a disjunct population in southwestern Nebraska.

A second sub-pattern is displayed by nine species which occur primarily in eastern and southeastern Kansas and southwestern Missouri where they inhabit rocky (especially calcareous) tallgrass prairies, limestone glades and bald knobs. Examples include *Aster sericeus, Camassia angusta* (Fig. 23), *Nemastylis geminiflora, Parthenium hispidum, Cissus incissa* and *Acacia angustissima* (Fig. 24). *Aster sericeus* (Fig. 25) is the only member of this series which extends north of Kansas.

Twelve species, including *Croton glandulosus, Eryngium leavenworthii, Mammillaria missouriensis, Liatris squarrosa* var. *glabrata, Callirhoe involucrata* and *Monarda citriodora,* occupy drier habitats than do the members of the previous two groups, and are more widely distributed than the members of those groups. Most of these species occur throughout central and eastern Kansas and some are found in Missouri; about half of them extend north of Kansas in the Great Plains.

The fourth group consists of 10 species which are more mesic than the three previous groups and which are more widely distributed than the first two groups. Seven of these are found primarily in the eastern half of Kansas and in much of Missouri, Arkansas, Oklahoma and Texas, but some extend northward into Nebraska and the Dakotas as well. Species in this group include *Cephalanthus occidentalis, Helianthus salicifolius, Ophioglossum engelmannii, Prunus mexicana* and *Marsilea mucronata.*

It is perhaps noteworthy that the southern species seem to be taxonomically distinct (more so than in any of the other major groups described). The only two exceptions to this would be *Berlandiera texana* and *Lesquerella gracilis.* These two have areas of distribution intermediate between the first and second sub-patterns described in this section, and it appears that there may be two varieties of each involved.

SOUTHWESTERN SPECIES

Eighty-two of the 479 species studied have their present center of frequency in the southwestern United States. These have a typical range of Arizona and New Mexico, east to Texas, north to Colorado and Kansas and sometimes extend into the northern Great Plains (Fig. 26). *Mimosa borealis, Prosopis juliflora, Prunus gracilis* and *Rhus trilobata* are the only woody

TABLE 5. Habitat preferences of southwestern species.

Habitat	No. species
1. Shortgrass prairie	36
2. Midgrass (often rocky) prairie hillsides	11
3. Sandy tallgrass prairie	31
4. Alkaline prairie	4
	82

species which come in with the southwestern flora. The southwestern species are most comonly found in the following habitats: shortgrass prairie; midgrass (often rocky) prairie hillsides; sandy prairie; and alkaline prairie (see Table 5). Those usually found in shortgrass prairie include *Aristida divaricata, A. longiseta, Baccharis wrightii, Buchloë dactyloides, Ditaxis humilis, D. mercurialina, Eriochloa contracta, Gaura villosa, Gilia acerosa, Triodia pilosa* and *Zinnia grandiflora.* Species which are found primarily on midgrass, often rocky, prairie hillsides include *Berlandiera lyrata, Castilleja citrina, Hybanthus verticillatus, Mimosa borealis, Oenothera greggii, Teucrium laciniatum* and *Rhus trilobata.* Examples of plants which occur on sandy prairie are *Artemisa filifolia, Baccharis salicina,Bouteloua eriopoda, Chloris virgata, Eriogonum longifolium, Gaillardia pulchella, Haplopappus annuus, H. ciliatus, Heliotropium convolvulaceum, Linum pratense, Penstemon ambiguus* and *Psilostrophe villosa.* Representatives of alkaline prairie plants are *Distichlis stricta, Eustoma russellianum, Panicum obtusum* and *Vernonia marginata.*

Within the southwestern group, there are three sub-patterns of distribution. Forty-two are found within the southwestern quarter of the state and do not occur north of Kansas. Some of these arc across the southwestern corner of the state. Others such as *Castilleja citrina* (Fig. 27) enter farther east in the red gypsiferous soil areas of extreme south-central Kansas or in the sandy soils south of the Cimarron and Arkansas rivers. Species placed in this group include *Aristida divaricata, Berlandiera lyrata, Convolvulus incanus, Dalea jamesii, D. lanata, D. nana, Eriochloa contracta, Eriogonum longifolium, Hilaria jamesii, Opuntia imbricata, Prunus gracilis* and *Zinnia grandiflora.*

A second group of 37 species occurs within the western half of the state. These tend to extend north of Kansas (Fig. 28). Included in this group are *Abronia fragrans, Aristida longiseta, Artemisia filifolia, Buchloë dactyloides, Engelmannia pinnatifida, Eurotia lanata, Gutierrezia sarothrae, Haplopappus annuus, Hedeoma drummondii, Iva xanthifolia, Lygodesmia juncea, Opuntia polycantha* and *Ratibida tagetes.*

A third minor pattern is exhibited by *Eustoma russellianum, Gilia longiflora* (Fig. 29) and *Sporobolus airoides* which are found in the sand hill areas of southwestern and south-central Kansas and then skip to the sand hills of Nebraska.

NORTHERN SPECIES

Only 13 of the 479 species studied have a center of frequency north of Kansas. Some span the continent from east to west, others are more centrally distributed, but all come into Kansas from the north (Fig. 30). Two of the 13 are woody; 6 are grasses. These species occur in the following general types of habitats: marshes; tallgrass prairie; shortgrass prairie; canyons, prairie hillsides, and streambanks; and alkali and salt flats (see Table 6).

TABLE 6. Habitat preferences of northern species.

Habitat	No. species
1. Marshes	1
2. Tallgrass prairie	2
3. Shortgrass prairie	6
4. Canyons, prairie hillsides and streambanks	3
5. Alkali and salt flats	1
	13

Spartina pectinata occurs in marshes; *Stipa spartea* and *Penstemon grandiflorus,* in tallgrass prairie; and *Hymenopappus filifolius, Linum rigidum* var. *compactum, Stipa viridula, S. comata* and *Poa arida* are species of shortgrass prairies. Plants usually found in canyons, on prairie hillsides or along streambanks include *Muhlenbergia racemosa, Rosa woodsii* and *Symphoricarpos occidentalis. Heliotropium spathulatum* is representative of species common on alkali and salt flats.

Within Kansas and the Great Plains, a tendency toward three subpatterns is apparent. *Heliotropium spathulatum, Rosa woodsii, Poa arida, Stipa comata* (Fig. 31) and *S. viridula* (Fig. 31) are primarily restricted to the western half of the plains, while *Penstemon grandiflorus, Spartina pectinata* and *Stipa spartea* (Fig. 31) occur in most abundance within the eastern half. *Muhlenbergia racemosa* is representative of the third and largest group of species which are widespread throughout the Great Plains but are more abundant in the north.

INTERIOR SPECIES

Of the species studied, 33 have an inland distribution which in general ranges from Michigan and Indiana west to Minnesota, Nebraska, Kansas, Oklahoma, Texas, Arkansas and Missouri (Fig. 32). Ten of these are woody. The plants in this group are more difficult to divide into habitat types than any other group, primarily because they occur in a wider variety of habitats.

TABLE 7. Habitat preferences of interior species.

Habitat	No. species
1. Moist woodlands, creek valleys and canyons	7
2. Open forest, thickets and rocky banks	8
3. Forest border, rocky hillsides and tallgrass prairie	8
4. Tallgrass prairie	1
5. Disturbed areas, fields and rocky hillsides	2
6. Sandy tallgrass prairie, hillsides and limestone glades	1
7. Moist tallgrass prairie, ditches and marshes	6
	33

The following list of habitat types reflects some of the difficulties involved: moist woodlands, creek valleys and canyons; open forest, thickets and rocky banks; forest border, rocky hillsides and tallgrass prairie; tallgrass prairie; disturbed areas, fields and rocky hillsides; sandy tallgrass prairie, hillsides and limestone glades; and moist tallgrass prairie, moist ditches and marshes (see Table 7). *Aesculus glabra* var. *arguta, Carex shortiana, Gymnocladus dioica, Viburnum prunifolium* and *Forestiera acuminata* are found in moist woodlands. Species which occur in open forest, thickets and on rocky banks include *Carex microdonta, Prunus hortulana, P. munsoniana, Pyrus ioensis, Rhamus lanceolata* and *Ribes missouriense.* Plants usually associated with forest borders, rocky hillsides and tallgrass prairie include *Amorpha canescens, Asclepias hirtella, Cornus drummondii, Clematis pitcheri, Echinacea pallida* and *Habenaria leucophaea. Phlox pilosa* var. *fulgida* is common in tallgrass prairie, and *Oenothera triloba* and *Heliotropium tenellum* are usually found in disturbed areas, fields and on rocky hillsides. *Liatris squarrosa* var. *hirsuta* occurs in sandy tallgrass prairies, hillsides and limestone glades, while *Carex arkansana, C. triangularis, Juncus interior* and *Bidens polylepis* are frequently found in moist tallgrass prairie, ditches and marshes.

Within Kansas, the interior species exhibit four of the same sub-patterns found within the group of eastern species. Some, including *Habenaria leucophaea, Pyrus ioensis, Rhamnus lanceolata* (Fig. 33) and *Ribes missouriense,* arc across the northeast corner of the state and tend to occur farther westward in Nebraska than in Kansas. Another subgroup of ten species including *Isoetes butleri, Forestiera acuminata, Carex triangularis,* and *Phlox pilosa* var. *ozarkana* arc across the southeastern corner of the state (Fig. 34). The remaining species enter Kansas directly from the east. Examples include *Carya texana, Viburnum prunifolium, Aesculus glabra* var. *arguta* (Fig. 35), *Asclepias hirtella, Bidens polylepis* and *Clematis pitcheri* (Fig. 36). *Liatris squarrosa* var. *hirsuta* (Fig. 37) enters from the east, but does not occur in the tallgrass prairie peninsula (previously described) which extends from the Flint Hills through east-central Kansas into Bates County, Missouri. As within other major groups of plants already described, there is a tendency for the interior species to skirt the High Plains areas of western Kansas and to cross the plains farther north in Nebraska.

WIDESPREAD SPECIES

Of the 479 species studied, 67 are so widespread in distribution that it seems impossible to associate them with any one of the centers of frequency already discussed. Some of these such as *Typha latifolia*, *T. angustifolia*, *Sorghastrum nutans* and *Salix interior* are abundant throughout much of their range. Others such as *Carex buxbaumii*, *Potamogeton gramineus*, and *Azolla mexicana* are collected only at scattered stations. *Acer negundo*, *Salix amygdaloides* and *S. interior* are the only woody plants placed in this group. The plants in this group occur in the following types of habitats: forest; forest border to grassland; streambanks and ravines; open areas of grassland, disturbed areas, and fields; marshes and other wet places; and in aquatic habitats (see Table 8). *Botrychium virginianum*, *Asplenium trichomanes* and *monotropa uniflora* occur most often in forests, while *Selaginella rupestris*, *Celastrus scandens*, and *Danthonia spicata* are usually found anywhere from forest border situations to grassland. *Acer negundo*, *Prunella vulgaris*, *Salix amygdaloides* and *S. interior* are found along streambanks and ravines. Species of moist open areas of grasslands, disturbed areas, and fields include *Carex buxbaumii*, *Cyperus acuminatus*, *Myosurus minimus*, *Juncus torreyi*, *J. dudleyi*, *Equisetum laevigatum* and others. Plants usually found in drier open areas in grasslands, disturbed areas and fields are *Leptoloma cognatum*, *Sorghastrum nutans*, *Leptochloa fascicularis*, *Glycyrrhiza lepidota* and *Festuca octoflora*. Plants which occur primarily in marshes or wet places include *Heteranthera limosa*, *Phragmites communis*, *Scripus americanus* and *Sparganium eurycarpum*. Aquatic species include *Azolla mexicana*, *Ceratophyllum demersum*, *Najas guadalupensis*, *Potamogeton diversifolius*, *P. foliosus* var. *macellus*, *P. gramineus*, *P. illinoensis* and *Ruppia maritima* var. *rostrata*.

TABLE 8. Habitat preferences of widespread species.

Habitat	No. species
1. Forest	7
2. Forest border to grassland	5
3. Streambanks and ravines	4
4. Open areas of grassland, disturbed areas and fields	31
5. Marshes and other wet places	8
6. Aquatic	12
	67

Within this group 17 species are northward and westward around the southern plains in the manner already described for species in other groups.

Species which display this pattern include *Acer negundo, Adiantum pedatum, Antennaria neglecta, Aster novae-angliae, Carex nebraskensis, Celastrus scandens, Danthonia spicata, Equisetum arvense, Koeleria cristata* and *Prunella vulgaris.*

The other 50 species present a miscellanea of individual patterns. All but one of the aquatic species studied fall into this group. These tend to have a scattered distribution, and are dependent primarily on the presence of ponds, lakes and other bodies of water. A number of relatively weedy species and plants of open habitats also are included in this group. Examples of these include *Draba reptans, Glycyrrhiza lepidota, Chloris verticillata,* and *Cuscuta pentagona.*

SPECIES ENDEMIC TO PORTIONS OF THE GREAT PLAINS

For purposes of this study, the Great Plains is defined as the region which extends from the eastern base of the Rocky Mountains to the deciduous forests of the east and from the Dakotas south to the northern edge of the Edwards Plateau in Texas. Of the 479 species studied, only six (from six different families) are *confined* to this region. None of the six occurs throughout but, instead, each is restricted to a smaller area within the Great Plains.

Three of the species—*Aster fendleri* (Fig. 38), *Oenothera fremontii* (Fig. 39) and *Scutellaria resinosa* (Fig. 40)—occur on chalk cliffs or dry, rocky calcareous hillsides and escarpments. *Clematis fremontii* (Fig. 41) which, as mentioned previously, has a disjunct population in east-central Missouri, is found primarily in the same type of habitat but sometimes occurs in rocky or dry midgrass prairie as well. *Phlox oklahomensis* (Fig. 42) occurs on gypsiferous soils in Woodward County, Oklahoma, the type locality, but in Kansas it is found in rocky limestone tallgrass prairie in the southern Flint Hills. *Juncus brachyphyllus* (Fig. 43), the most widely distributed of these Great Plains species, is a sandy tallgrass prairie plant which also occurs on upland sandstone glades and sandy prairies in Missouri.

The distributions of taxa closely related to these species suggest that at least three of them may have been associated at one time with floras to the south of Kansas. According to Erickson (1945), *Clematis fremontii* var. *riehlii* is restricted in Missouri "to glades, rocky barrens which occur on south- and west-facing slopes of otherwise wooded ridges." Floristically, Erickson relates these glades to the shale barrens of the Appalachians, to the cedar glades of the Nashville basin in Tennessee, to portions of the grasslands of Kansas and Nebraska, and to glade-like grassy areas in the Arbuckle Mountains of Oklahoma and the Edwards Plateau of Texas. On the basis of the distribution of other plants associated with the glades, particularly *Oenothera missouriensis,* Erickson theorizes that "the two *Clematis* populations may have been connected by way of the Edwards Plateau. The separation into two populations may have occurred during the semi-arid period of the late Pleistocene, or, in view of the importance of competition from grasses, during the warmer, moister period which followed."

Scutellaria resinosa also has affinities to the south. It occurs in Kansas, where it is morphologically distinct and homogeneous, and also in northern Texas and western Oklahoma, where it becomes more variable and difficult to distinguish from *S. wrightii*. The latter species occurs primarily in the Edwards Plateau region, where it is morphologically distinct, and extends into north-central Texas and southwestern Oklahoma (Epling, 1942).

Wherry (1955) regards *Phlox oklahomensis* as a descendant of an offshoot from *P. speciosa* var. *occidentalis* (now restricted to the western and northwestern United States) which migrated far southeastward. "Destroyed in most of its range by the Pleistocene ice steets and xerothermic maxima, it managed," according to Wherry, "to survive the last of these in the western Ozark region, and has subsequently been spreading northwestward." Another possibility might be that the ancestral species was centered in northern Mexico and/or the southwest and migrated northward in two directions—northwestward along the west coast and northeastward through Texas and Oklahoma to Kansas.

DISCUSSION AND CONCLUSIONS

With distribution data available for 479 species, one is tempted to speculate about the factors which define areas of distribution and, certainly, about the origins of the Kansas flora. There are, however, certain inherent dangers in such speculation. When attempting to arrive at broad generalizations it is always possible to misplace emphasis or to arrive at unwarranted conclusions because of the fragmentary knowledge of the distribution and biology of many species. Nevertheless it does seem possible and worthwhile to interpret the major recurring patterns and sub-patterns in the light of past geological events and present environmental conditions.

Although the species studied have been divided into groups according to their centers of frequency, one finds that some sub-patterns are duplicated by members of more than one group. It would appear that once species reached the plains area, they adjusted genetically to the environment without regard to their origin or to the species group with which they arrived. Each species has developed some degree of tolerance which has enabled it to compete and survive in the new association of which it has become an integral component.

One of the most interesting patterns revealed is the northward and westward arc across the Great Plains, a pattern displayed by species from the east, northeast, southeast, and interior groups as well as by a number of widespread species. Braun (1955) mentions this distribution pattern briefly but does not consider it in detail. Of 56 plants which follow this pattern, 45 are elements of either forest, forest border to open areas, streambanks and marshes or moist grasslands. The southern edge of this arc, as mentioned previously, corresponds roughly with the southern limits of glaciation in Nebraska and seems to reflect present climatic and edaphic conditions as well. For many species, the southern edge of this arc passes through the sand hills of Nebraska, a tallgrass prairie region characterized primarily by a dune topography with little surface drainage. The loose sandy soils deposited over Brule clay during the Pliocene and Pleistocene (Tolstead, 1942) readily absorb rain water, thus reducing water loss by runoff and evaporation. The impenetrable layer of clay beneath the sand keeps the water table relatively close to the surface and results in numerous springs and shallow lakes. The sandhills are also located in a region which, according to Borchert (1950), has a somewhat less variable summer rainfall from year to year than does the surrounding plains region. If one plots the mean annual water loss due to transpiration and evaporation in percent of rainfall for the central states (Fig. 44), there can be seen a westward extension of the 95% isopleth in northern Nebraska and South Dakota, bridging the plains area between eastern Nebraska and the sandhills and corresponding roughly with the arching pattern of some plant species. North of Nebraska, increased relative humidity, reduced average temperatures and shorter growing season increase effectiveness of rainfall even though the amount of prepicitation which falls is actually less than in the southern plains. These factors together create mesic conditions in the midst of an area which—with an average annual rainfall of 18 inches and with high temperatures, low humidity, prevailing south winds and frequent droughts during the summer—actually has a semi-arid climate. South of the arc, there are few habitats which mitigate the effects of the xeric southwestern climate sufficiently to allow for the survival of these mesic species. Collections of some of these species to the south into Kansas indicate that they are rare in the area and are either disappearing or are occasionally introduced and should be thought of as waifs.

As a group, the species which have disjunct populations within the arc are even more mesic (and hence more restricted in occurrence) than those which are continuous throughout the arc. Plants from the eastern deciduous forest (and from the Rocky Mountains to the west) find suitable habitats in the precipitous canyons of the Niobrara River and in the Black Hills. Both areas are supplied with springs and streams and afford protection from hot, drying prairie winds. Humidity within the canyons is higher than that of the surrounding uplands, and summer temperatures are lower. The more mesic nature of these areas also reduces damage from winter drought. It seems likely that these mesic species migrated across the prairie during the early Hypsithermal Interval of the Pleistocene, at which time they were probably more widespread than at present. During the later and drier Hypsithermal Interval, they apparently became localized in canyons and river valleys and perhaps in moist swales among higher sand dunes where they occur today as disjunct colonies.

The species which enter Kansas from the north seem to be limited primarily by the same factors which most influence distribution of species from the east—relative humidity, average temperatures and rainfall effectivity, among others. It is interesting to note that some introduced species have been observed to migrate into Kansas from the north. Gates (1940) reported *Carduus nutans* (nodding thistle) from Washington and Marshall counties. Since 1945, the species has increased in abundance. It has become a serious pest over all of eastern Kansas and by 1968 had moved into Oklahoma. It would be interesting to know whether this progressive movement has been due to development and natural selection of races tolerant of more southern environment or if it is merely a migration.

A third pattern—the tendency to occur through central Missouri and across the southeast corner of Kansas—is displayed by species from the east, northeast, southeast and interior groups. These species in general are taxonomically distinct. There are a number of factors, some seemingly unrelated to one another, which share parallel arching boundaries through southeast Kansas, angling eastward or northeastward through Missouri. Among these are elevation, topography, surface geology and soils (Schoewe, 1949). Climatic maps by Borchert (1950) reveal clines in amount of winter rainfall, percent of normal precipitation which falls during drought years and average departure from normal temperature in July of major drought years which seem to correlate with (or at least to coincide with) this distribution pattern. For some plants, the northern boundary in Missouri is the Missouri River or the approximate limit of maximum glaciation which, in that state at least, roughly parallels the climatic clines described by Borchert. Steyermark (1959), Braun (1955) and others have discussed plant distribution in relation to the glacial boundary in some detail. For some species, it is possible to point to glaciation as a causal mechanism for existing distribution patterns. For other species, the correlation seems to be a geographical one but not necessarily a causal one. Often, however, there is a tendency to assume that there *must* be some sort of cause and effect relationship present which we are unable to see and then, of course, to continue looking for such a connection. Perhaps this is being too narrow-minded. If we believe Gleason's (1922) statement that the "glacial climate differed from the modern not so much in kind as in degree," then it seems possible that climatic patterns during the Pleistocene were similar to those illustrated by Borchert for the present. Might it not be that the same climatic factors which presently influence distribution patterns also limited the southward extent of the glaciers and hence the location of the glacial boundary? In particular, we are thinking of the warm dry southwesterly winds which prevail throughout much of the year in the Great Plains, along with high summer temperatures, low humidity and other factors which represent the influence of the southwest upon the climate of the Great Plains. If this were true, the boundaries of both the glaciers and the species ranges would be due to the same climatic factors, rather than the species boundary being dependent upon the glacial boundary.

The general area of distribution of the interior species suggests that these plants may have survived in the Ozarkian region of Missouri and northern Arkansas during the Pleistocene glaciations and late Hypsithermal Interval and have since radiated out from that region. Presently, they occupy a region where the assigned limits of the eastern, northeastern, southeastern, southern, northern and Great Plains centers of frequency come together. The interior species occur in a larger number of habitats than any other group described, although the individual species tend to be rather conservative in habitat preference and occur in fewer habitat types.

The southwestern and southern species are thought to be the oldest members of the Kansas flora and ones which were the least affected in their distribution by the Pleistocene glaciations. It seems likely that the ancestors of the southwestern species were members of the Madro-tertiary flora which came into the plains region during the late Tertiary. Being better adapted for a xeric habitat, they were able to migrate into the Prairie Peninsula during the late dry Hypsithermal Interval. Relict colonies of prairie which remain scattered through the midwestern states today include the following southwestern and southern species: *Opuntia fragilis, Sporobolus heterolepis, Cristatella jamesii, Callirhoe triangulata, Agave virginica, Galactia volubilis, Salvia lyrata* and *Ophioglossum engelmannii.* In the loess mounds along the Missouri River in northeastern Kansas and northwestern Missouri, some exposed slopes and tops of hills are occupied by species more characteristic of areas to the west. Included among these are *Bouteloua hirsuta, B. gracilis, Yucca glauca* var. *glauca, Cleome serrulata, Dalea enneandra, Glycyrrhiza lepidota, Euphorbia marginata, Liatris punctata* var. *nebraskana, Aster sericeus, Lygodesmia juncea* and *Oxytropis lambertii.* According to Steyermark (1963), "the incursion of this plains flora into these areas may have taken place in relatively recent times during a period sometime subsequent to the final retreat of the glaciers and perhaps within the past four thousand years."

Thus far in the discussion very little has been said about species which occur throughout the Great Plains, yet it is from these plants that we gain valuable information concerning the biological phenomena of adaptation and speciation.

One of our first attempts to correlate distribution patterns with present climate involved comparing the distributions of various species with zones of plant hardiness as mapped by the Arnold Arboretum (Fig. 45). We could find but few species whose distribution seemed to coincide in any way with the hardiness zones. Most of the species cross at least five zones, and many occur across seven or eight zones. A closer look at morphological and physiological variation (features which are not evident on dot maps) within these species aids in interpretation of this problem.

In areas such as California and Arizona where altitudinal and climatic changes are abrupt, speciation is thought to occur rather rapidly. In the Great Plains, however, where there are few marked regional differences in surface or elevation, latitude is the chief control of mean temperature and associated aspects of the climate such as insolation and length of growing season (Borchert, 1950). In the plains, there is a relatively even south-to-north transition in mean temperature and an east-to-west decrease in precipitation. The responses of plants to these clines are also transitional and, although physiologically evident, may not always be morphologically (and thus taxonomically) detectable. Much more work needs to be done on these phenomena.

Riegel (1940), studying variations of blue grama grass *(Bouteloua gracilis)*, observed that plants from the south produced the greatest growth in height for the season, and those from the north, the least. The southern plants also produced the most and coarsest textured foliage, while those plants of the northern section produced the least and finest. The roots of the southern group of plants penetrated to the greatest depth, while those of the northern plots (with the exception of Montana) were the shallowest. The southern plants produced the most spikes per flower stalk and the largest spikes on the tallest stalks, while the northern plants produced fewer and smaller spikes on shorter flower stalks. The northern plants began to flower on June 25 to July 1 and the southern ones began July 23 and 24. Those from the central group showed a wide variation in flowering time. Since these differences were observed in an experimental garden where all individuals were exposed to the same environmental conditions, one would assume that the variations are genetically fixed in response to differences in the environments from which the seeds were obtained.

McMillan (1959), studying ecotypic variation in 12 species of grasses native to the great plains, discovered three general flowering patterns which were detectable in a transplant garden. The first—displayed by *Koeleria cristata, Bouteloua gracilis, B. curtipendula, Panicum virgatum, Andropogon scoparius,* the *Andropogon gerardi-hallii* complex, *Sorghastrum nutans* and

Sporobolus heterolepis—showed early flowering for clones from the northern and western communities and later flowering toward the south and east. The second, exhibited only by *Elymus canadensis,* presented earliest flowering of clones from southern communities. In the third, flowering was simultaneous for clones from all communities represented. Species which displayed this pattern were *Stipa spartea, S. comata* and *Oryzopsis hymenoides.* McMillan describes these three as "opportunistic species, which resume growth and flower as soon as conditions permit." In McMillan's study, "shorter stature was correlated with the early maturity of northern and western material and was replaced by taller growth of the later-flowering forms toward the south and east. Correlations of height and maturity were not shown by *Elymus canadensis,* the only species with earlier maturity in southern species-populations."

In the transplant garden at the University of Kansas, clones of *Andropogon gerardi* and *A. scoparius* from northwestern Kansas consistently flower before those from the southeastern corner of the state. This corresponds directly with the length of growing season in the native habitat of each clone. In addition, plants from the eastern part of the state are always taller than those from the west, and the same differences in robustness and numbers of flowers as described by McMillan can also be noted.

It would appear that little correlation between the distribution of plains species and hardiness zones is apparent because the plains species migrated into the area and then evolved in place as the climate evolved. Hardiness zones, on the other hand, reflect the ranges of tolerance of cultivated species which, for the most part, are not native to this area. Perhaps more correlation between distribution of native plants and these temperature zones would be evident if more were known about physiological variation within species of the Great Plains.

In some groups, morphological differences as well as physiological ones can be detected, and these shed additional light on the problem of post-Pleistocene plant migrations and relationships. Unfortunately, there have been but few taxonomic and biosystematic studies of species complexes within the Great Plains. One of the more enlightening of these is the work of Harms (1963) on *Variation in the Heterotheca (Chrysopsis) villosa Complex East of the Rocky Mountains.* His study was based on field observations, analysis of mass population samples, growth of transplants and seedlings under uniform garden conditions, progeny tests, pollen analysis, determination of chromosome numbers and analysis of meiosis, artificial crossing, hybrid analysis, and a critical study of many herbarium specimens. His study of transplants and plants grown from seed indicate that variation in the group is genetic.

In the southern areas of the Great Plains, the *Chrysopsis villosa* complex appears as several distinct or nearly distinct diploid races. In the northern plains, the *C. villosa* forms are mostly tetraploid and intergrade so extensively that they can hardly be separated in any practical taxonomic manner. The origin of the tetraploid *villosa* is highly speculative, since this taxon tends to morphologically bridge the gaps between the presently known diploid species.

It is probable that some of the variation now present in *villosa* is due to a primary divergence in which different adaptive peaks have been reached in different areas of the range, since the geographical form is approached clinally without extreme variation being encountered in local populations. The tendency for correlation of *C. angustifolia* characters and the great variability everywhere accompanying the intergradation of *angustifolia* with *villosa* races strongly suggests a secondary intergraduation of taxa once well under way toward separate speciation.

According to Harms, the present variation patterns of *C. villosa* east of the Rocky Mountains allow several tentative speculations relating to its post-Pleistocene history. Non-introgressed populations of *C. hispida* in the Driftless Area of Wisconsin and the *hispida* influence which is apparent elsewhere in populations north of the Arkansas River suggest that this member of the complex was the first to move into the northern plains after the Wisconsin glaciation. During the Xerothermic Period, it withdrew northward and westward and was replaced by *villosa* which was spreading at that time from the foothills of the southern Rocky Mountains or perhaps from a refuge farther south. The two groups may have come in contact with one another at that time. At the same time that *villosa* was moving northward, races of *angustifolia* and *stenophylla* were expanding, presumably from a Texas refuge. Races of *foliosa* also began to move across the southern plains, perhaps from two refuges—one in the southwest and one in Texas. They have since come in contact with one another again and have intermixed. There has also been extensive hybridization and introgression between *villosa* and *angustifolia* and between *angustifolia* and *foliosa* during post-Pleistocene times. This complex series of factors makes taxonomic recognition most difficult.

Other taxonomic problems suggest that detailed biosystematic studies of plants within the Great Plains could yield information useful in the interpretation of post-Pleistocene plant migrations—information which, conversely, could be applied to further biosystematic studies. In the genus *Liatris*, for example, there are several species complexes which, if carefully worked out, might shed additional light on this problem. *Liatris spicata*, *L. pycnostachya* and *L. lancifolia* were recognized by Gaiser (1946) as distinct species. They are, however, morphologically quite similar. According to Gaiser and most manuals, *L. spicata* is eastern in distribution, occurring from New York to

Florida, westward to the Mississippi River. *L. pycnostachya* is primarily southeastern, but extends northward into Kansas, Nebraska and South Dakota. *L. lancifolia* is described as being southwestern, distributed from New Mexico northward to Kansas, Nebraska and South Dakota. These distribution patterns, together with field observations of their morphology, suggest that the situation is not as simple as Gaiser describes it, however.

In the *Liatris squarrosa* complex, Gaiser includes six varieties, two of which occur in the Great Plains. *L. squarrosa* var. *glabrata* occurs from Texas north to South Dakota and through most of its range shows little variation. *L. squarrosa* var. *hirsuta* has an area of distribution centered in Missouri and eastern Kansas and is much more variable than *glabrata*. Gaiser described a number of specimens which she assumed to be intermediates between *glabrata* and *hirsuta*, and Steyermark (1963) includes *L. squarrosa* var. *glabrata* in his *Flora of Missouri*. In our field work, however, we have not been able to find *glabrata* east of the Flint Hills nor *hirsuta* west of them. Plants in Missouri which tend to be glabrous although otherwise resembling *hirsuta* seem to indicate hybridization with another species, *Liatris cylindracea*, which occurs from western New York and southern Ontario west to southern Ohio, northern Indiana, Michigan, Minnesota and thence south to Arkansas. The few specimens of *glabrata* from eastern Oklahoma which have been observed suggest that here is an area where *glabrata* is more variable than it is farther north and an area where it might come into contact with colonies of *hirsuta*. Further work with this group promises to reveal information regarding Pleistocene and post-Pleistocene relationships and migrations.

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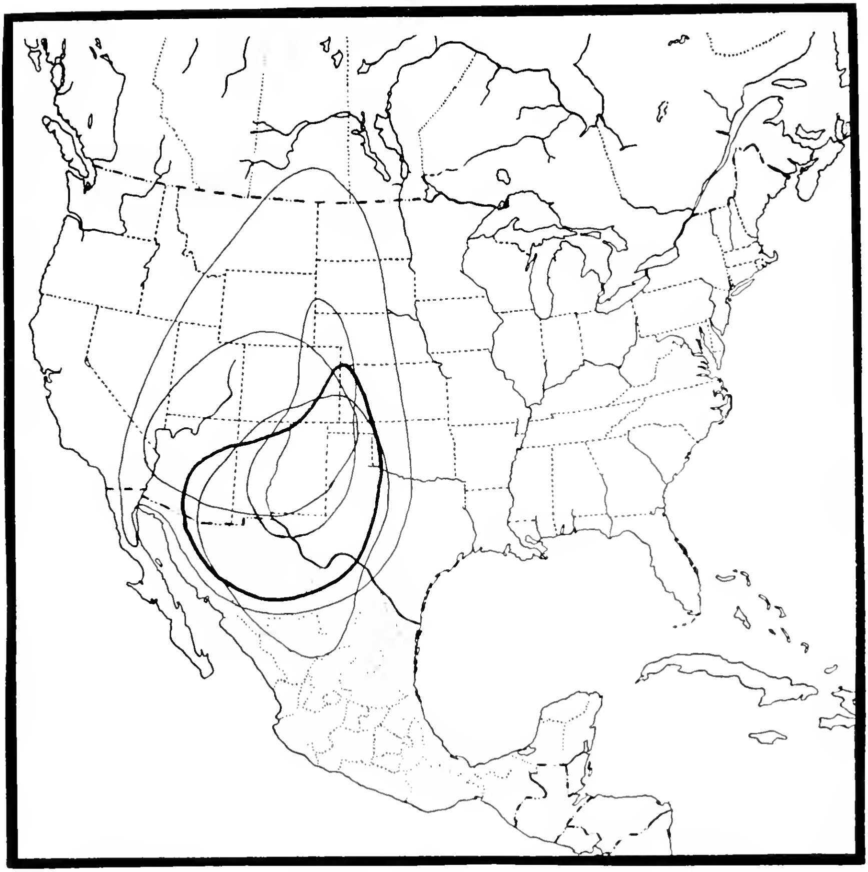

Fig. 1. Composite map showing typical distribution of southwestern species (heavy black line) and individual distributions of four southwestern species which extend into Kansas (thin black lines).

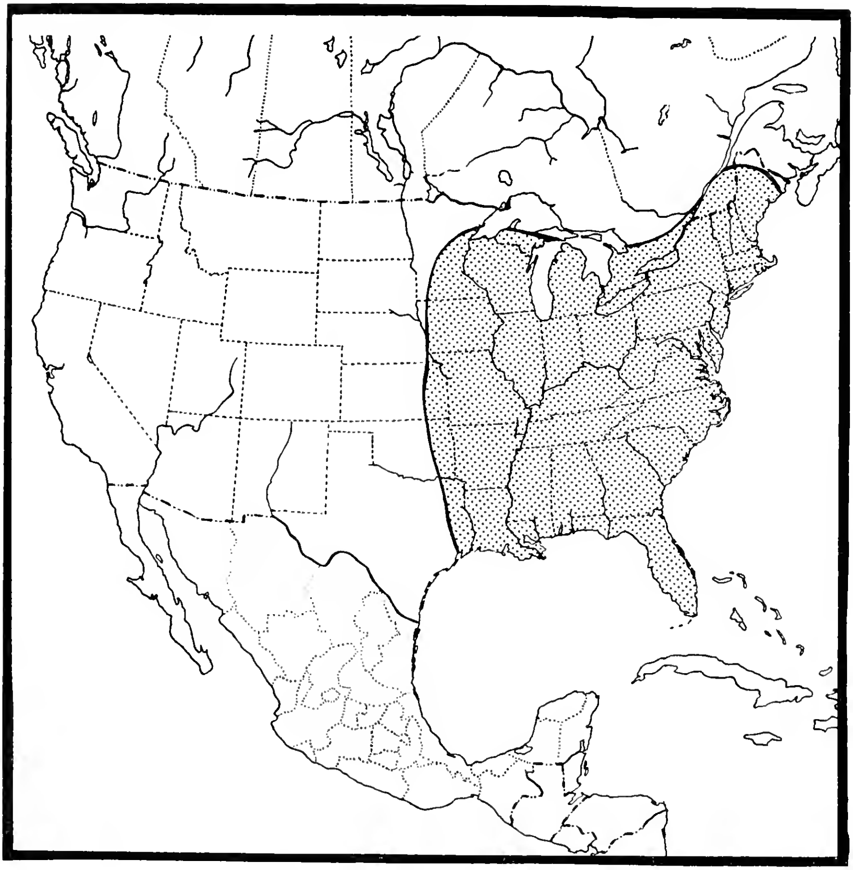

FIG. 2. General distribution of eastern species.

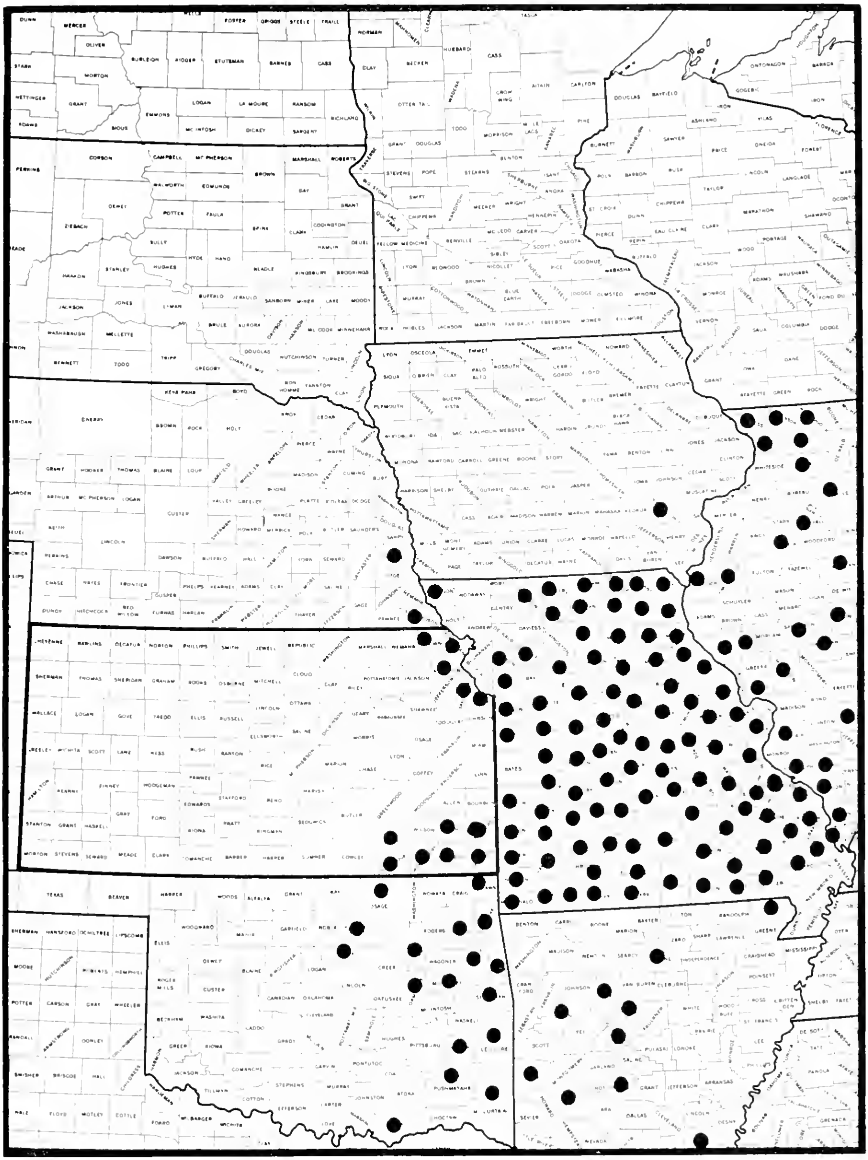

FIG. 3. *Amelanchier arborea*

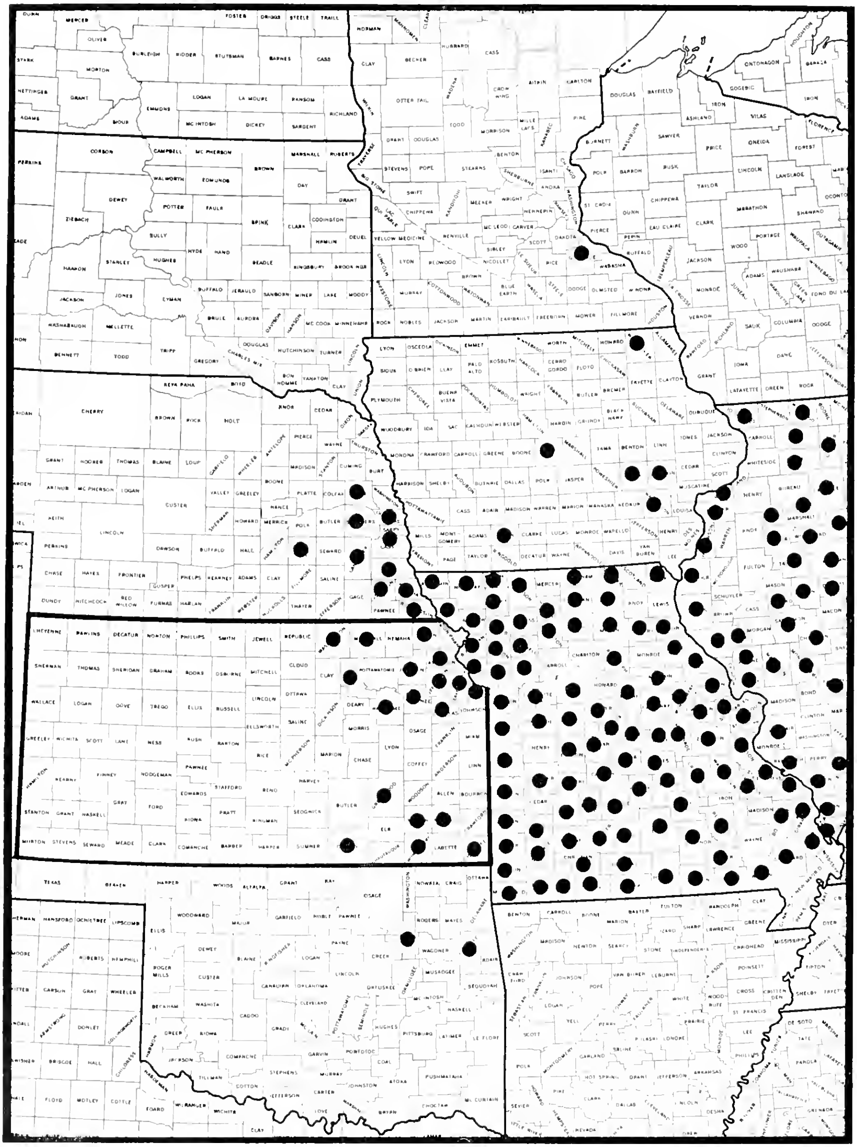

FIG. 4. *Dicentra cucullaria*

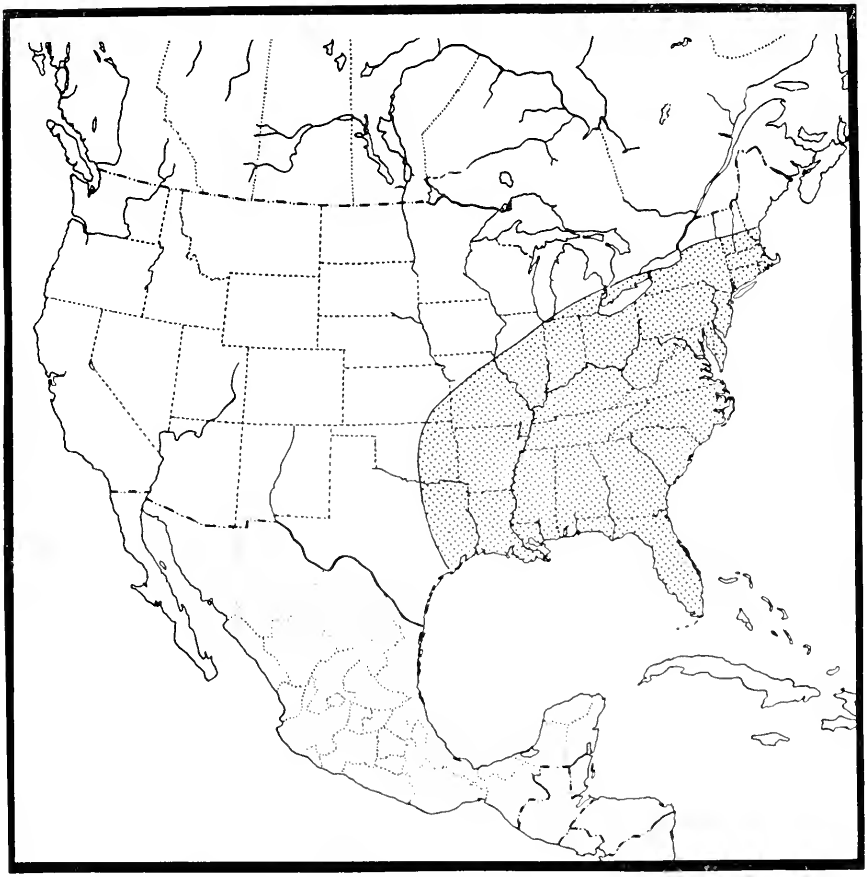

Fig. 5. Distribution of eastern species which are restricted to the southeast corner of Kansas.

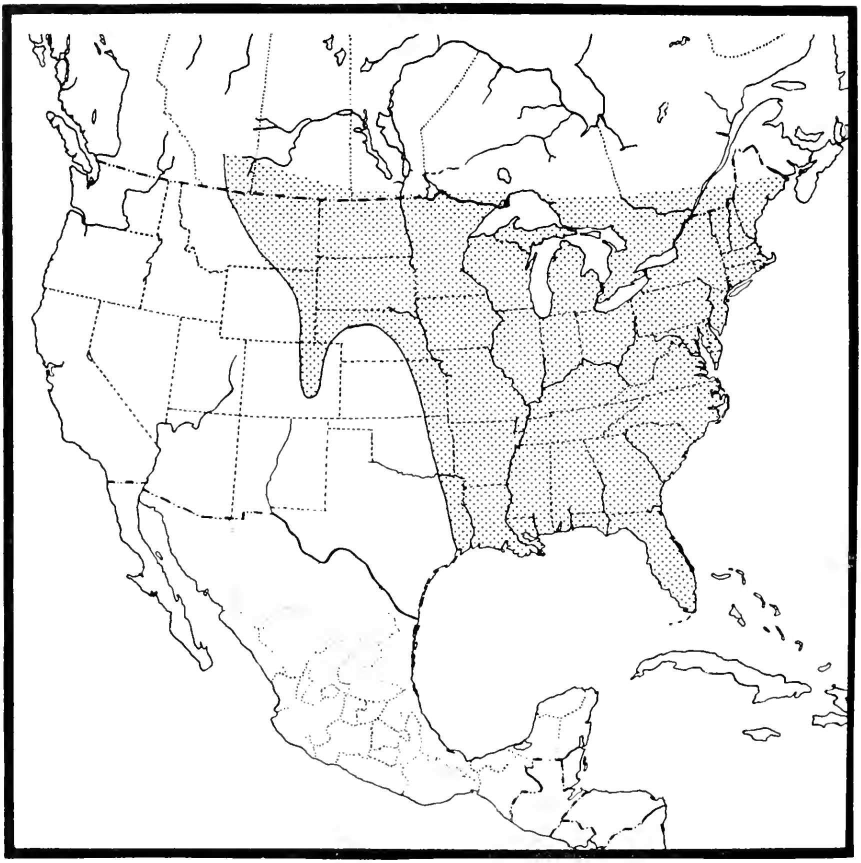

FIG. 6. Distribution of eastern species which are northward and westward around the southern Great Plains.

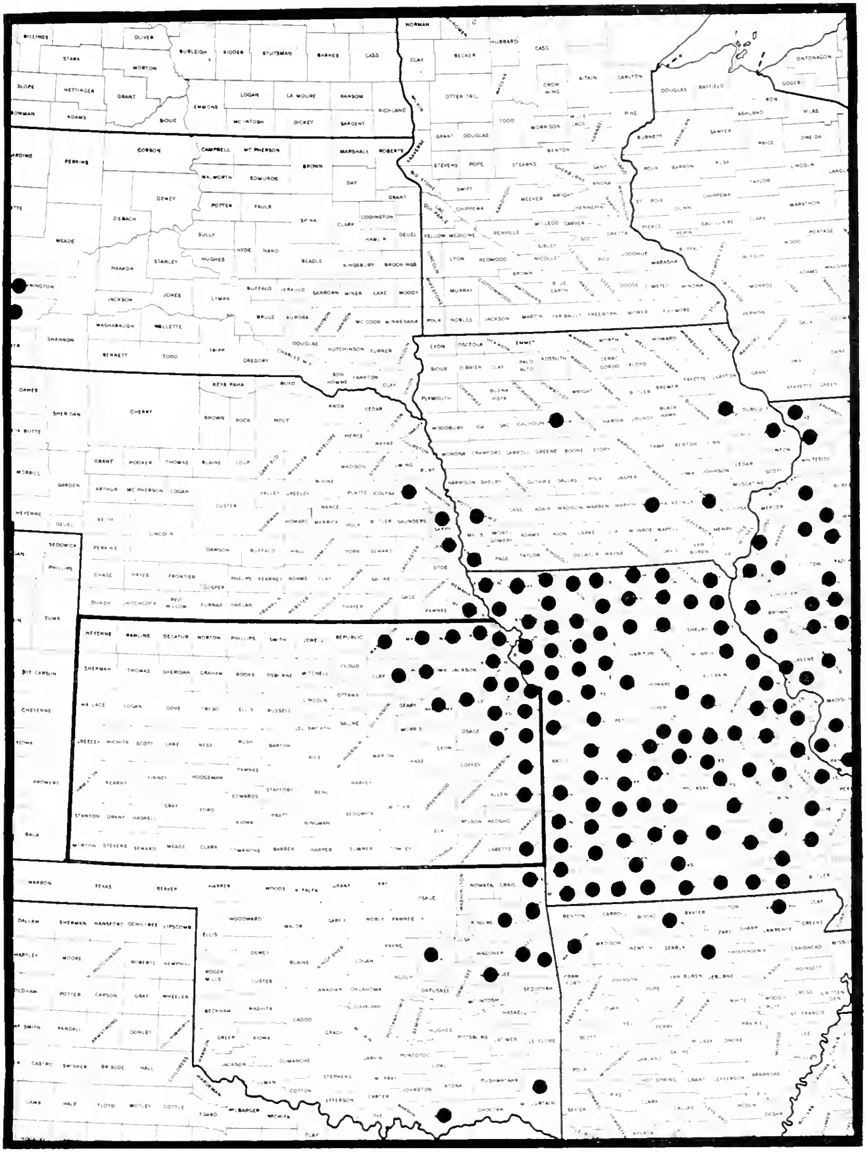

Fig. 7. *Anemone virginiana*

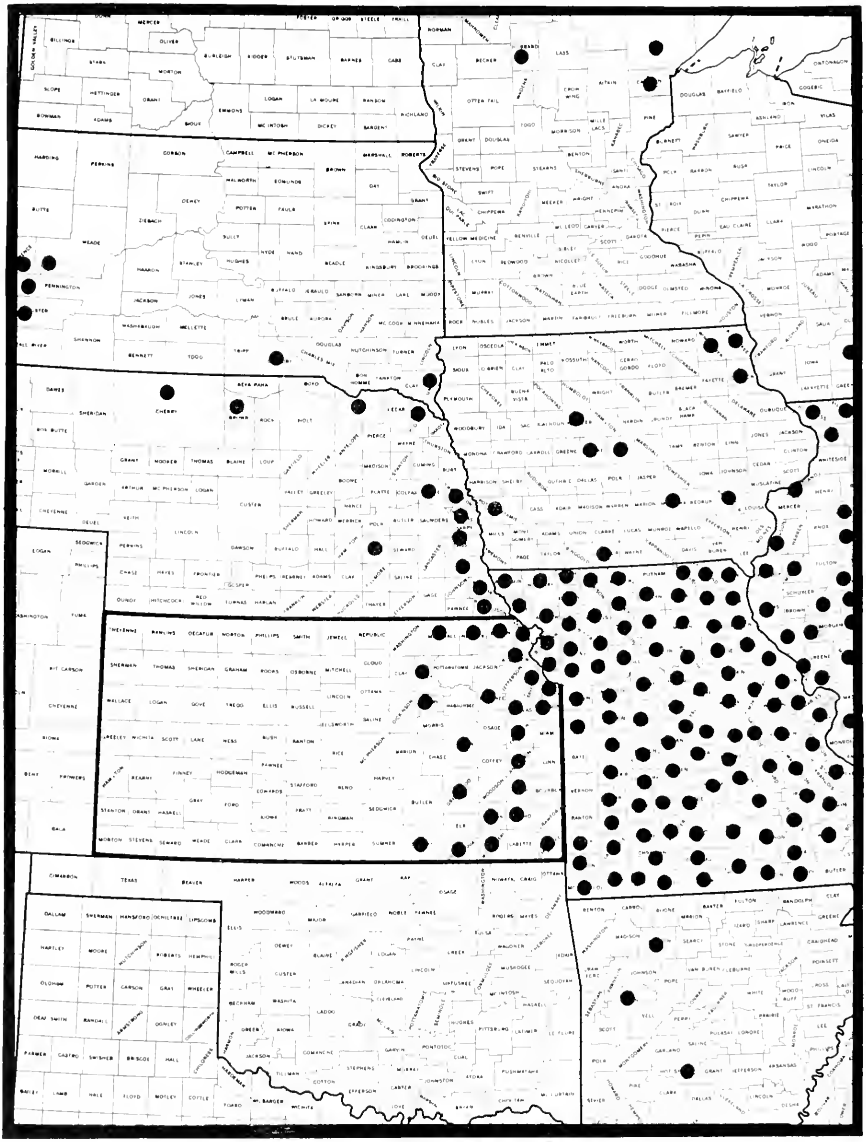

FIG. 8. *Aquilegia canadensis*

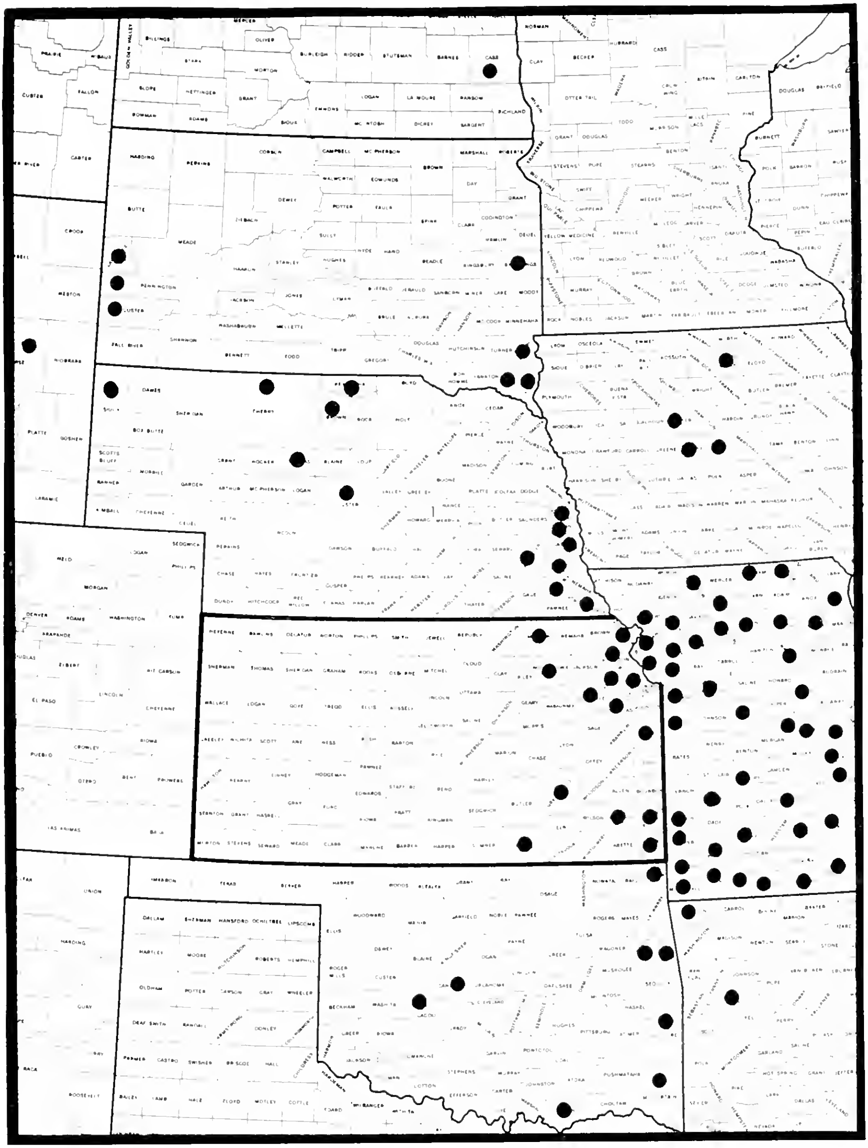

Fig. 9. *Osmorhiza longistylis*

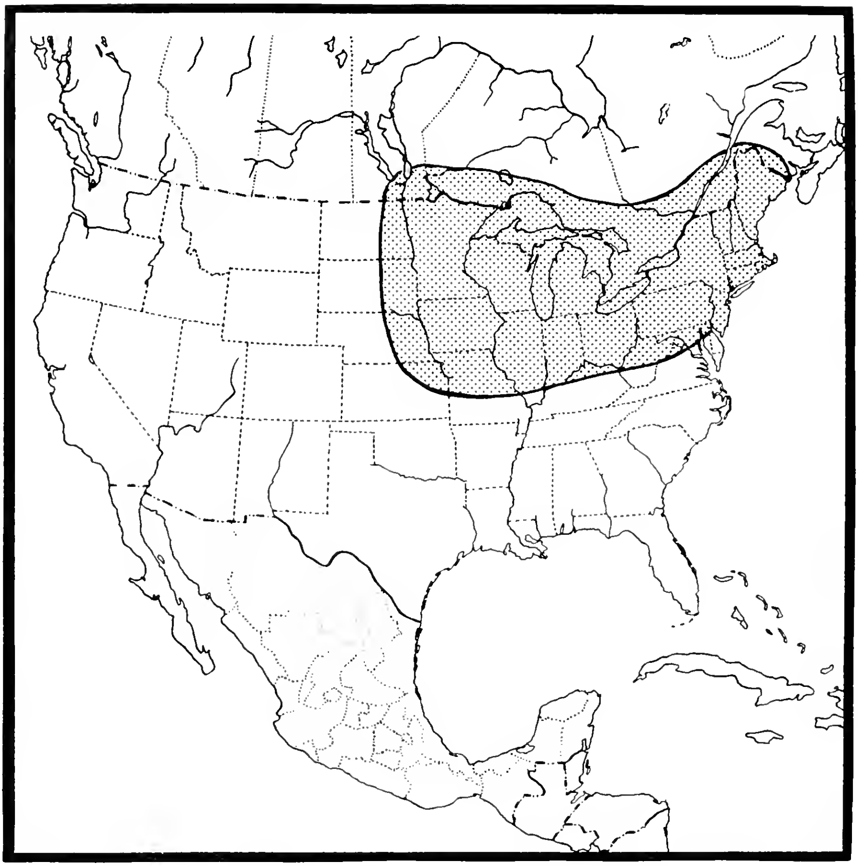

FIG. 10. General distribution of northeastern species.

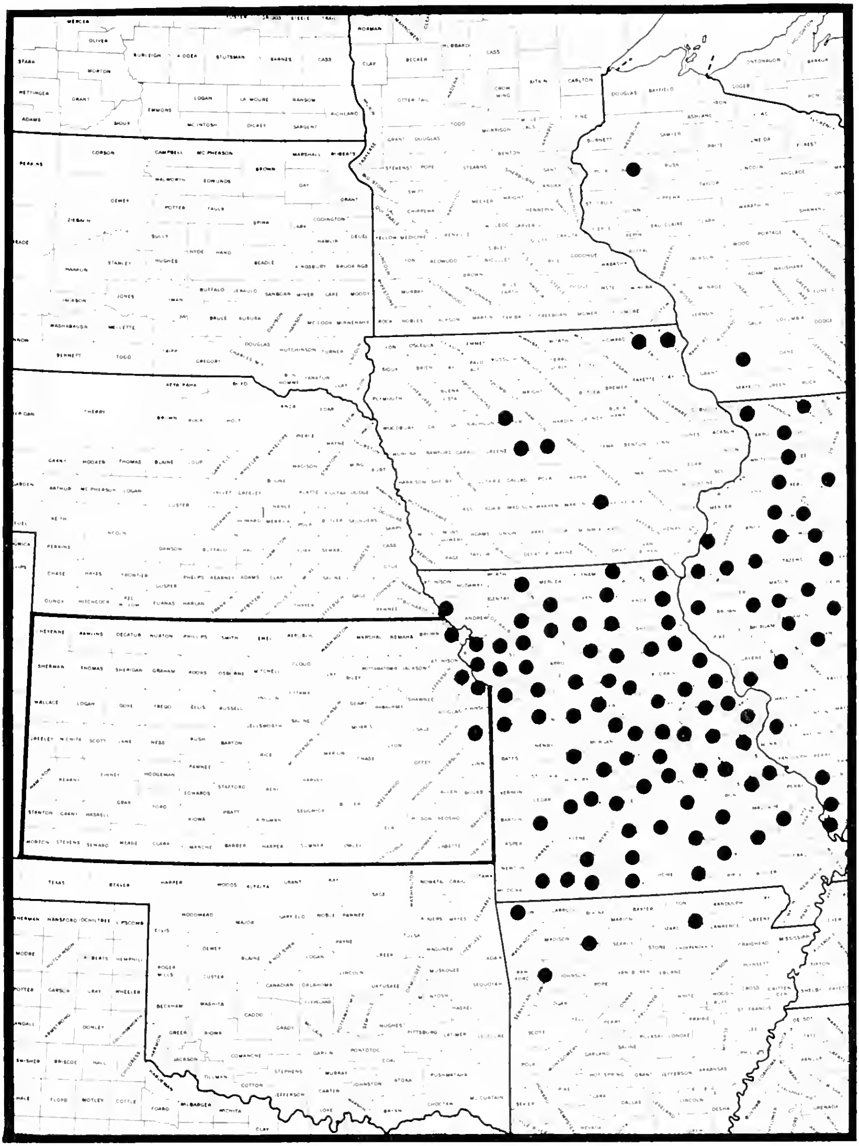

Fig. 11. *Hydrophyllum appendiculatum*

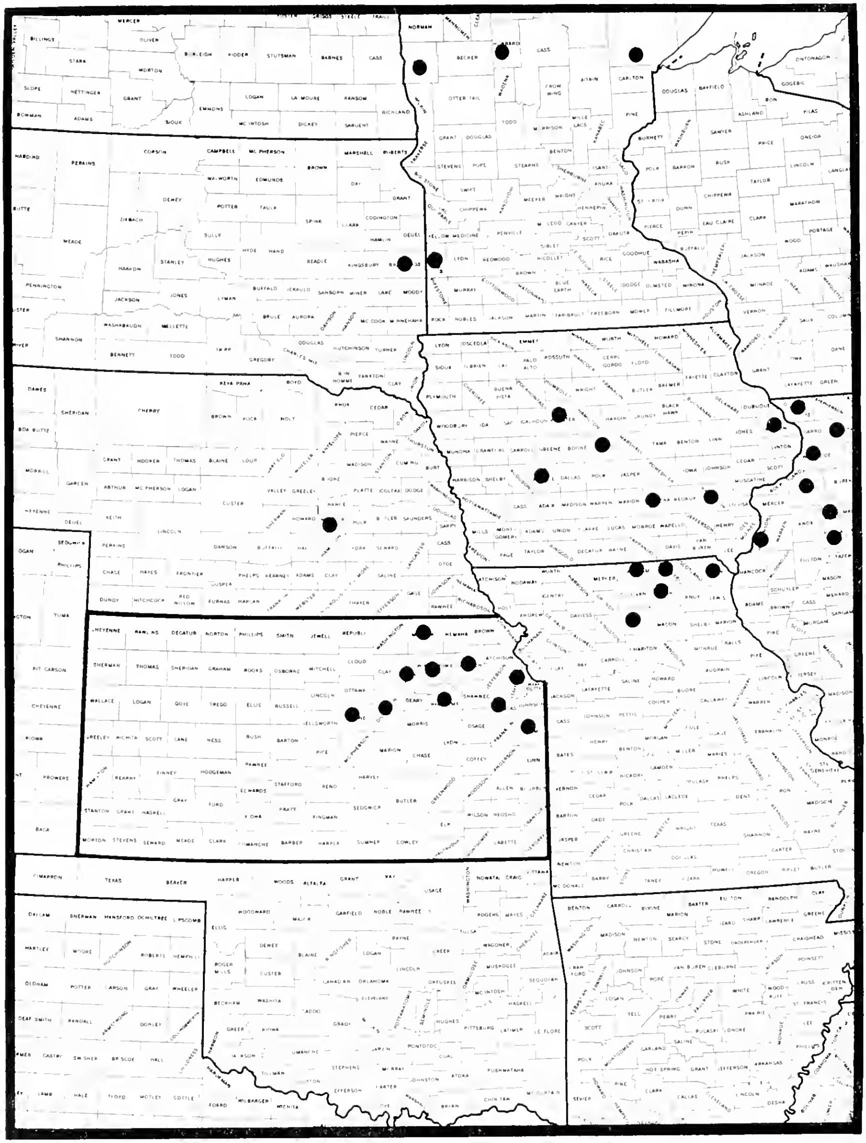

FIG. 12. *Rosa blanda*

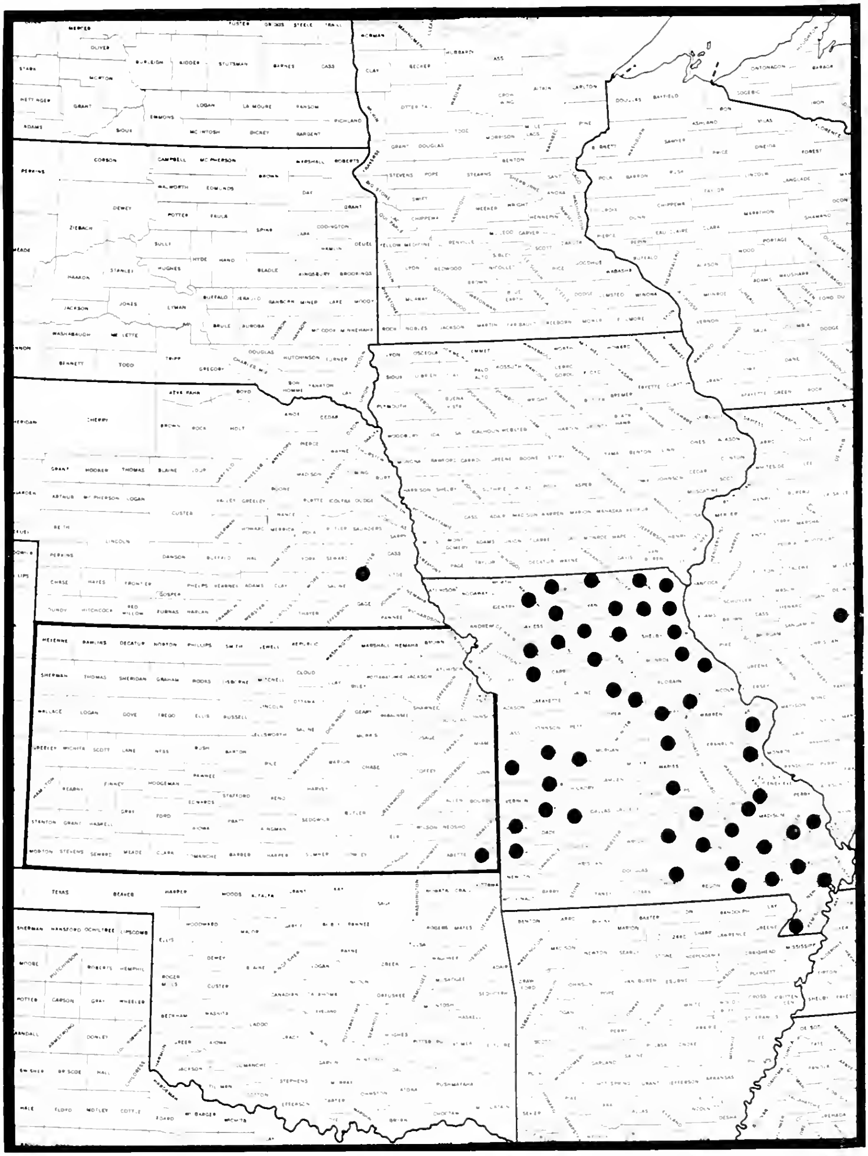

Fig. 13. *Carex squarrosa*

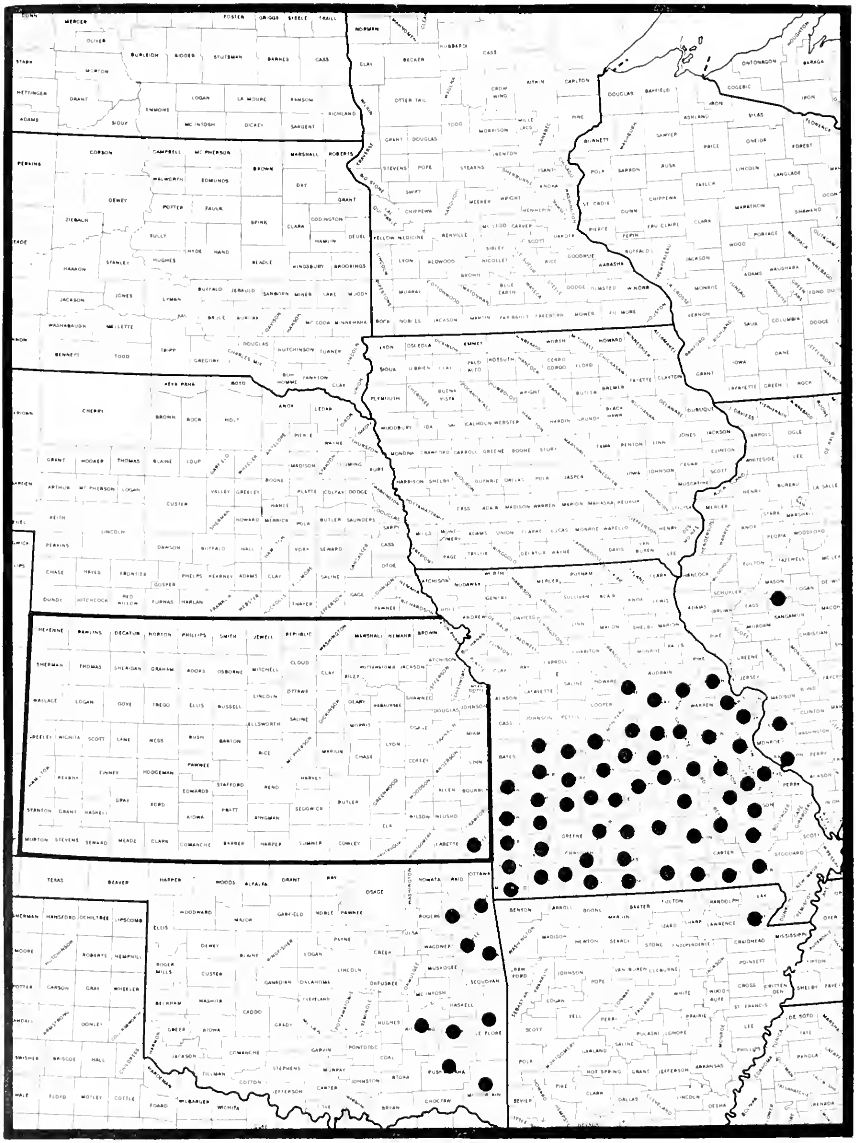

FIG. 14. *Vaccinium vacillans*

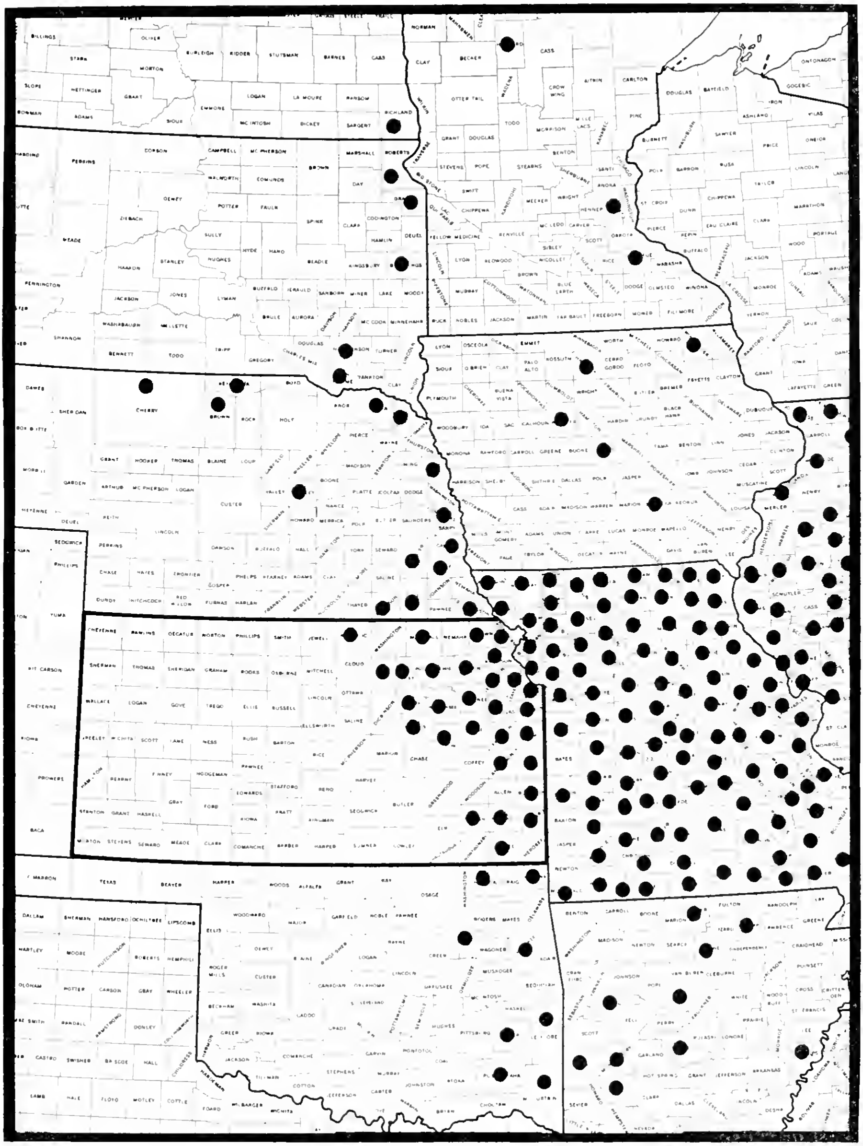

Fig. 15. *Tilia americana*

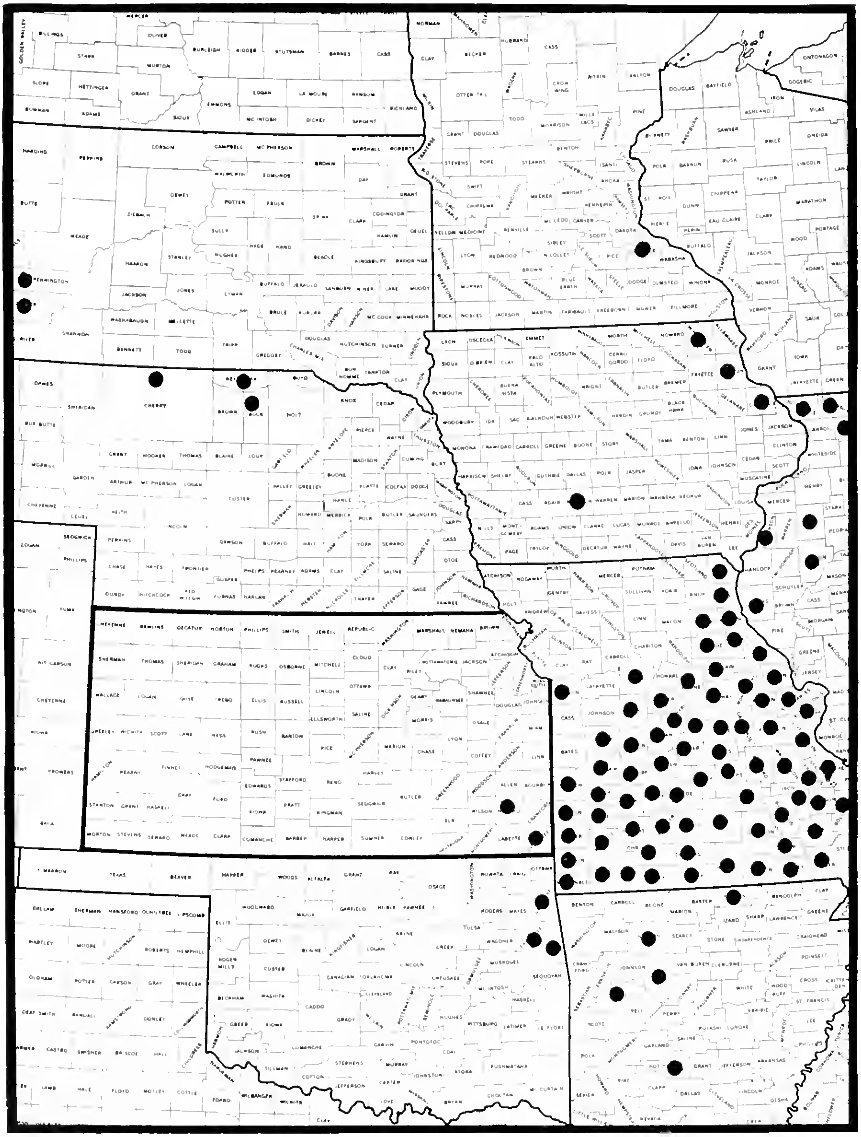

FIG. 16. *Physocarpus opulifolius*

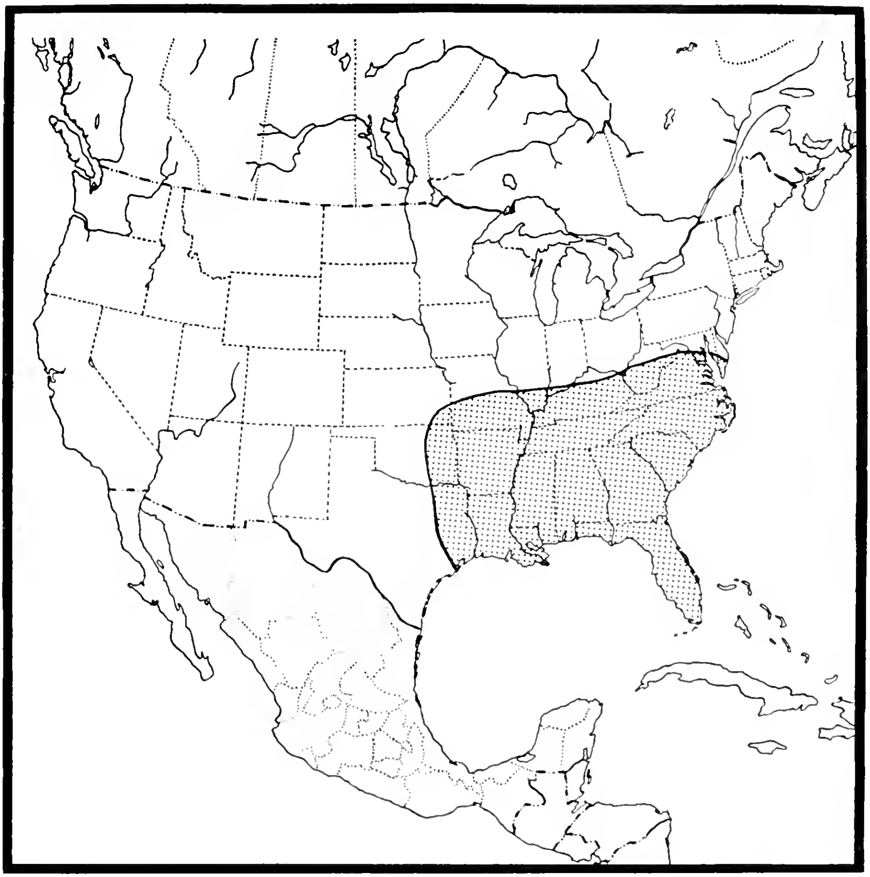

Fig. 17. General distribution of southeastern species.

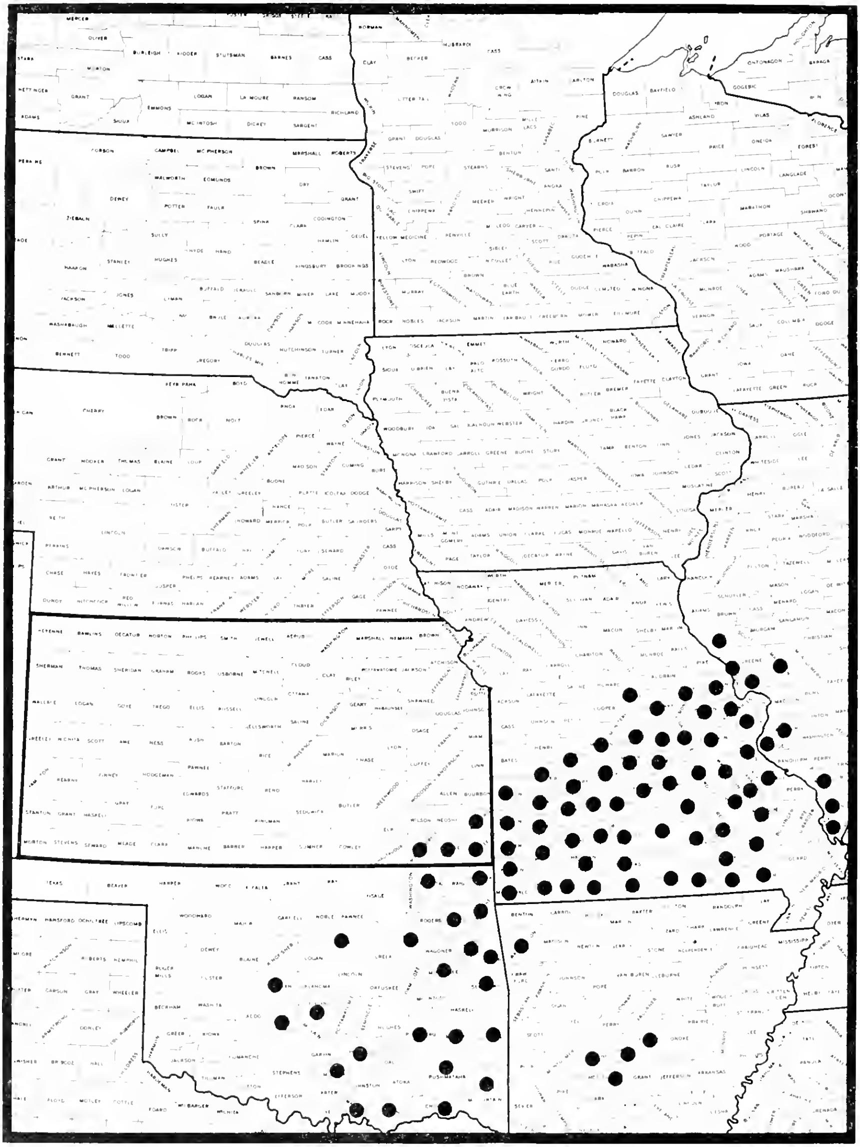

FIG. 18. Distribution of *Passiflora lutea* in the central states, showing typical arc across southeast Kansas.

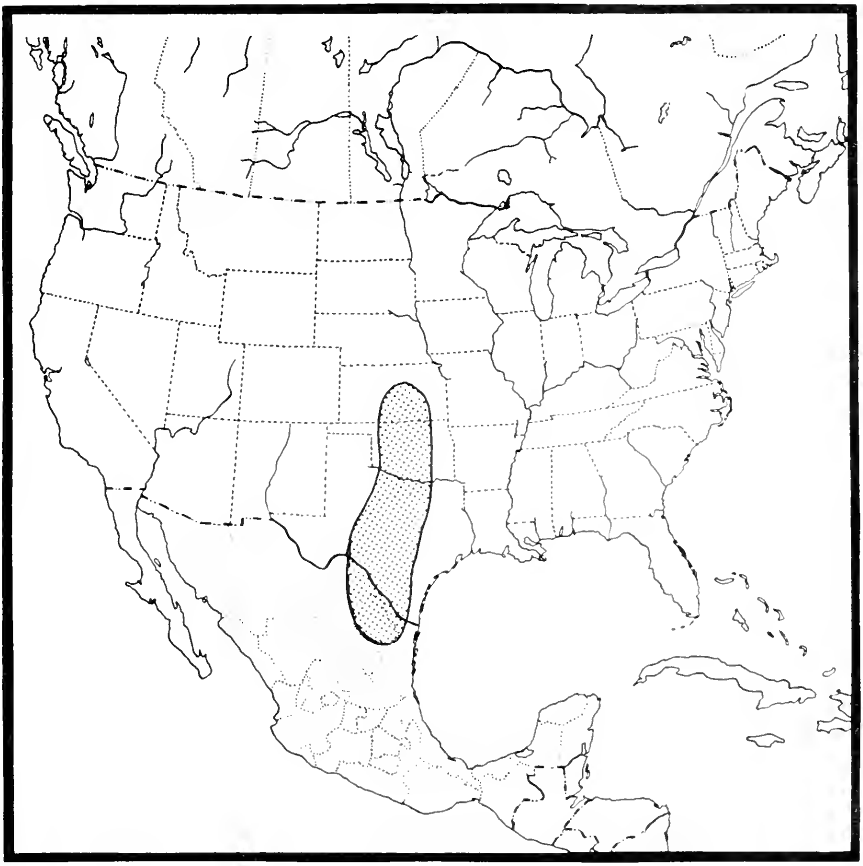

Fig. 19. General distribution of southern species.

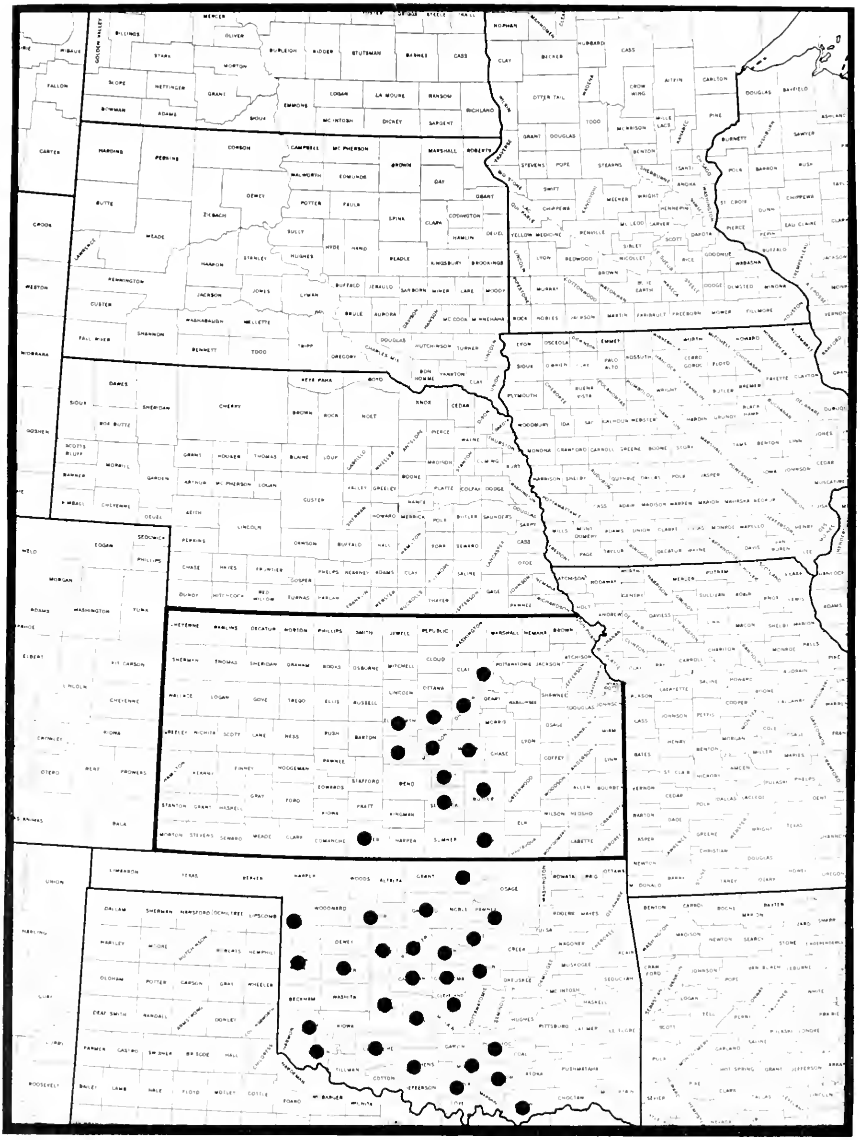

FIG. 20. *Androstephium coeruleum*

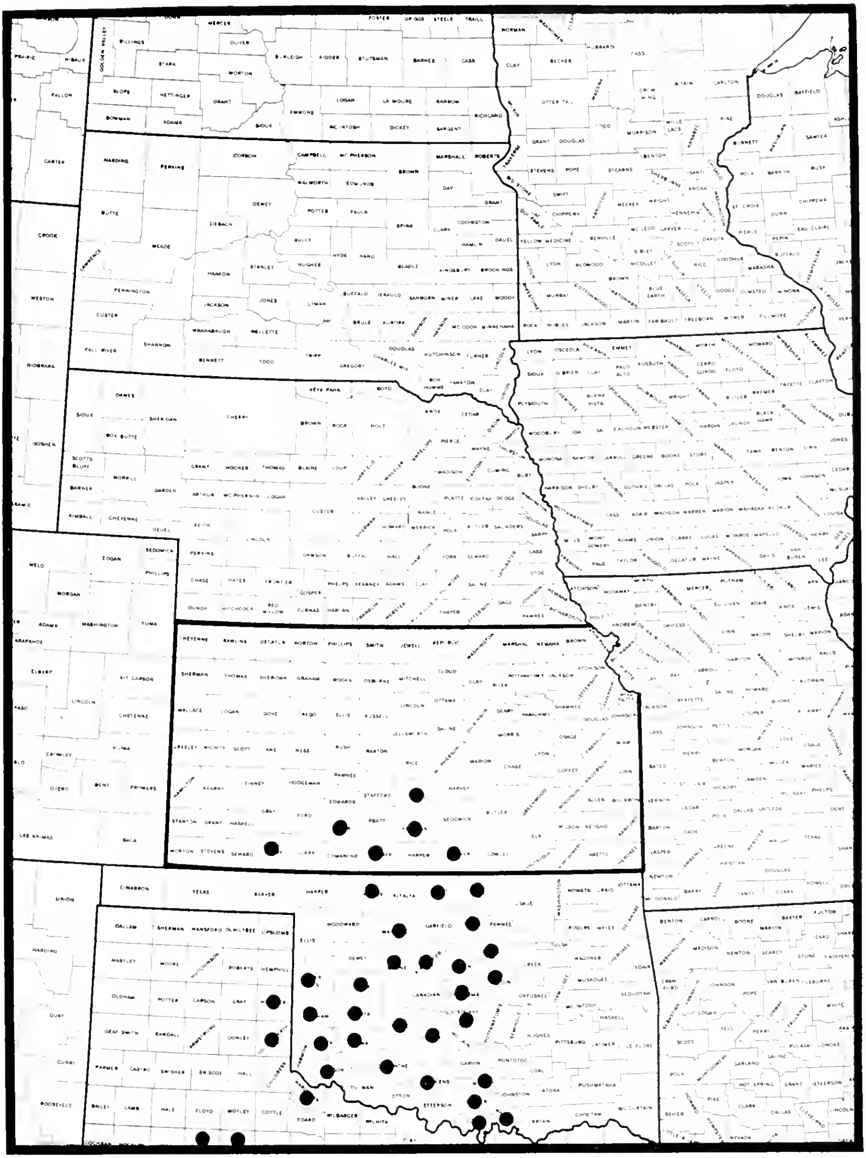

Fig. 21. *Gaillardia suavis*

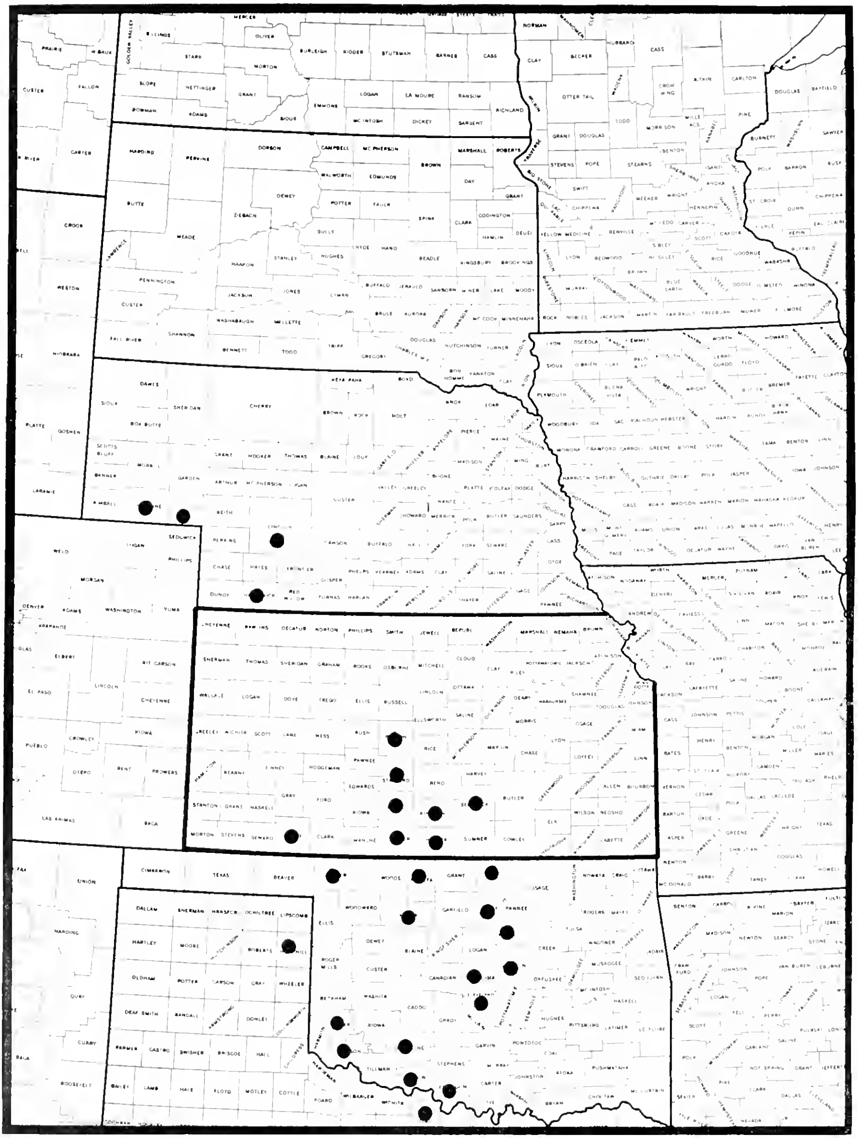

FIG. 22. *Cleomella angustifolia*

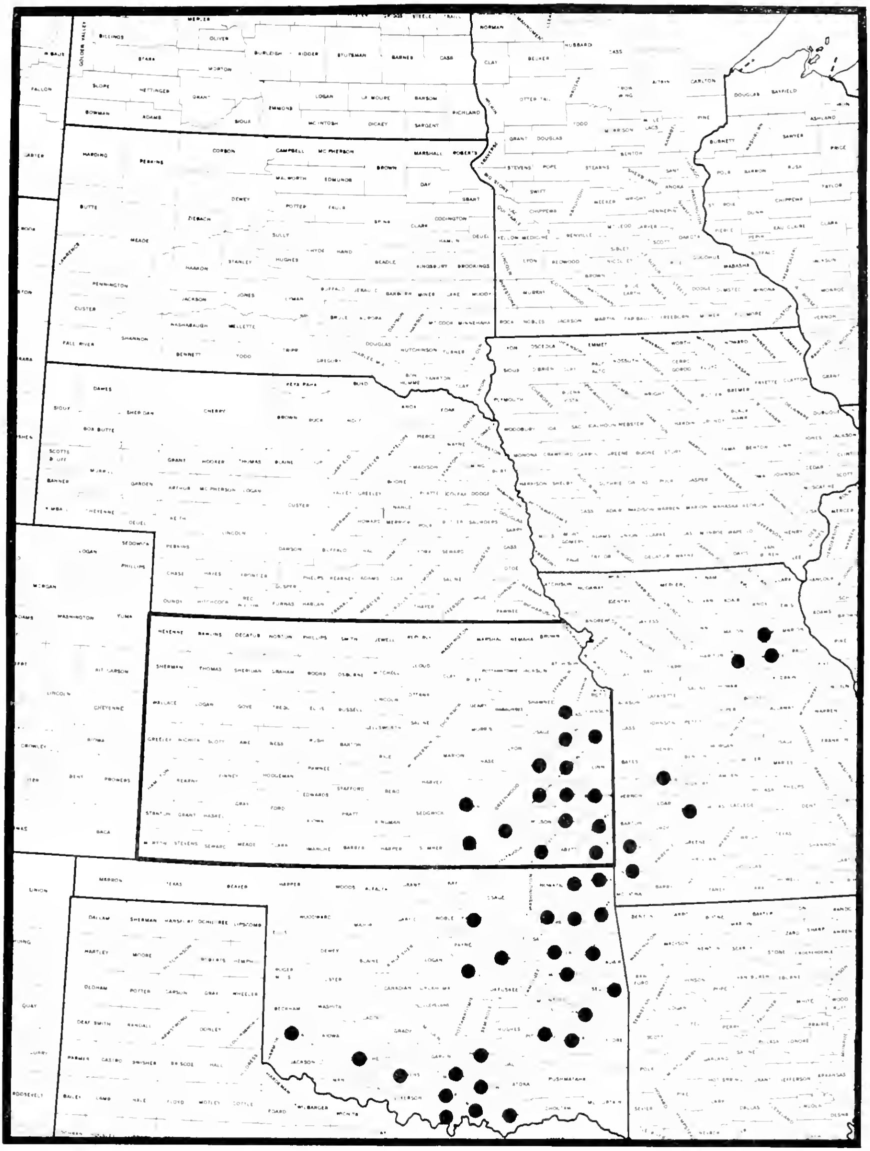

Fig. 23. *Camassia angusta*

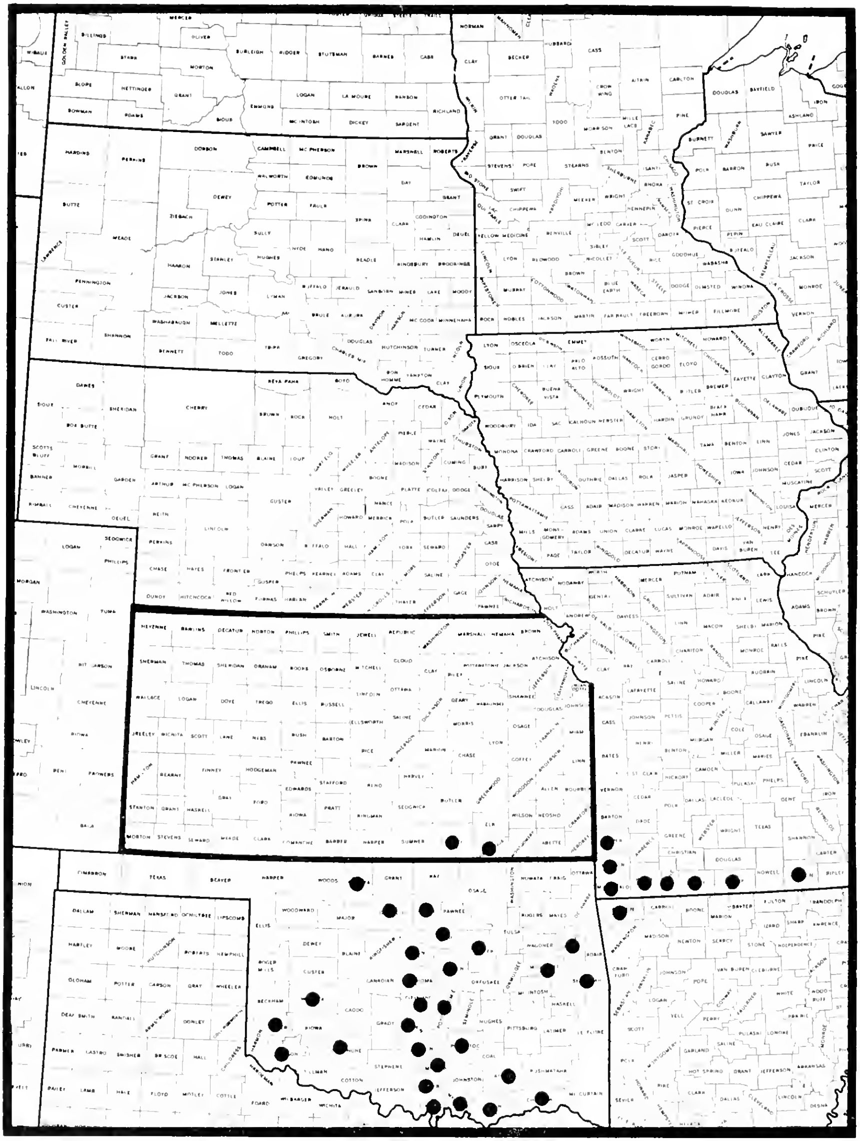

FIG. 24. *Acacia angustissima*

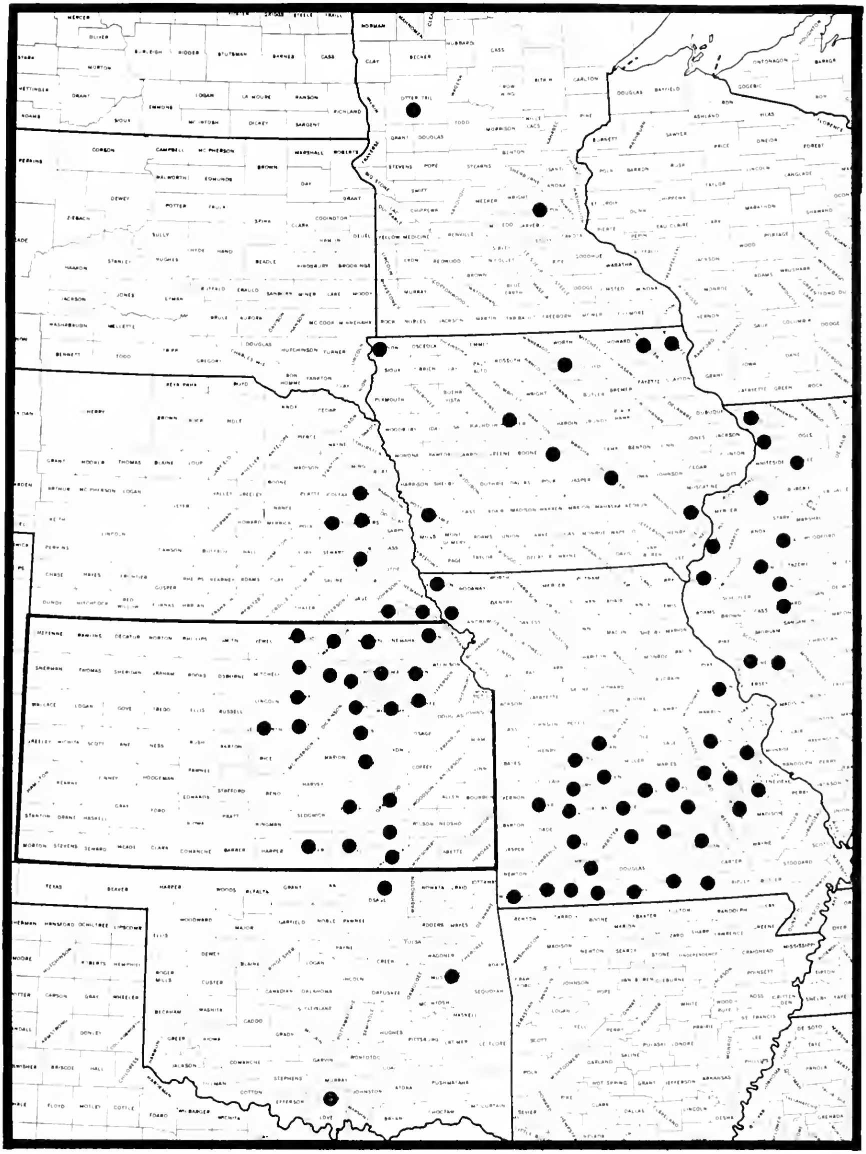

FIG. 25. *Aster sericeus*

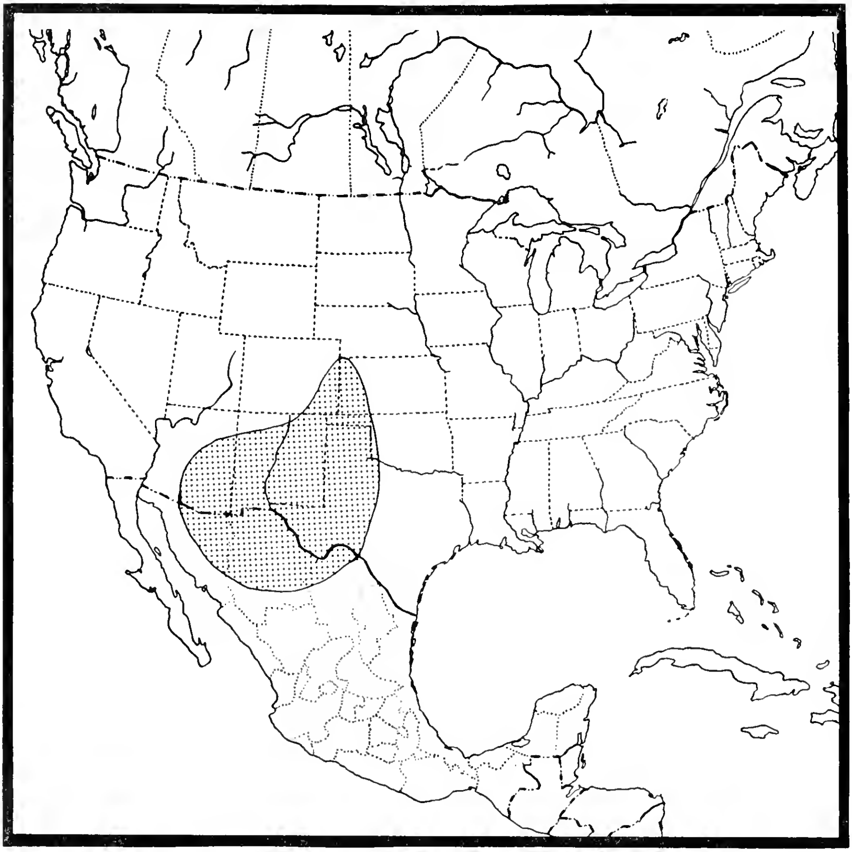

FIG. 26. General distribution of southwestern species.

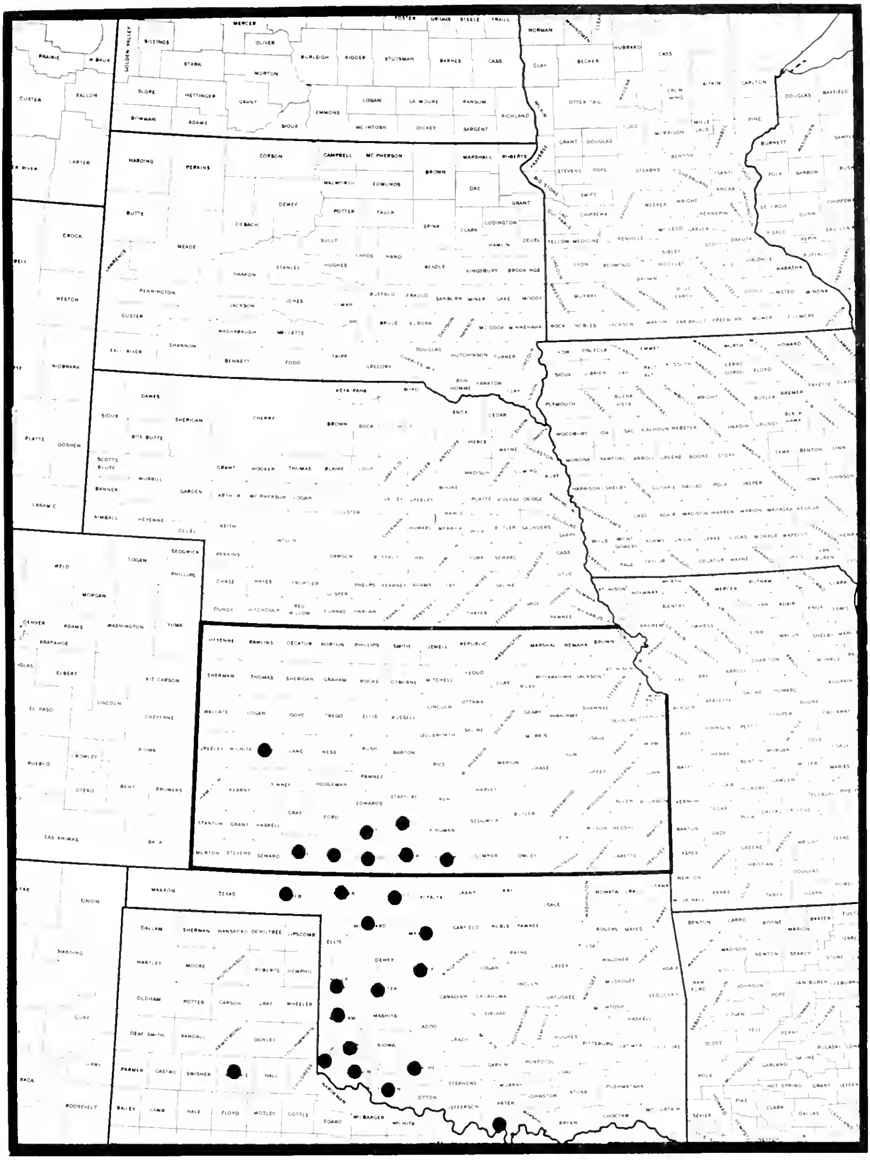

Fig. 27. *Castilleja citrina*

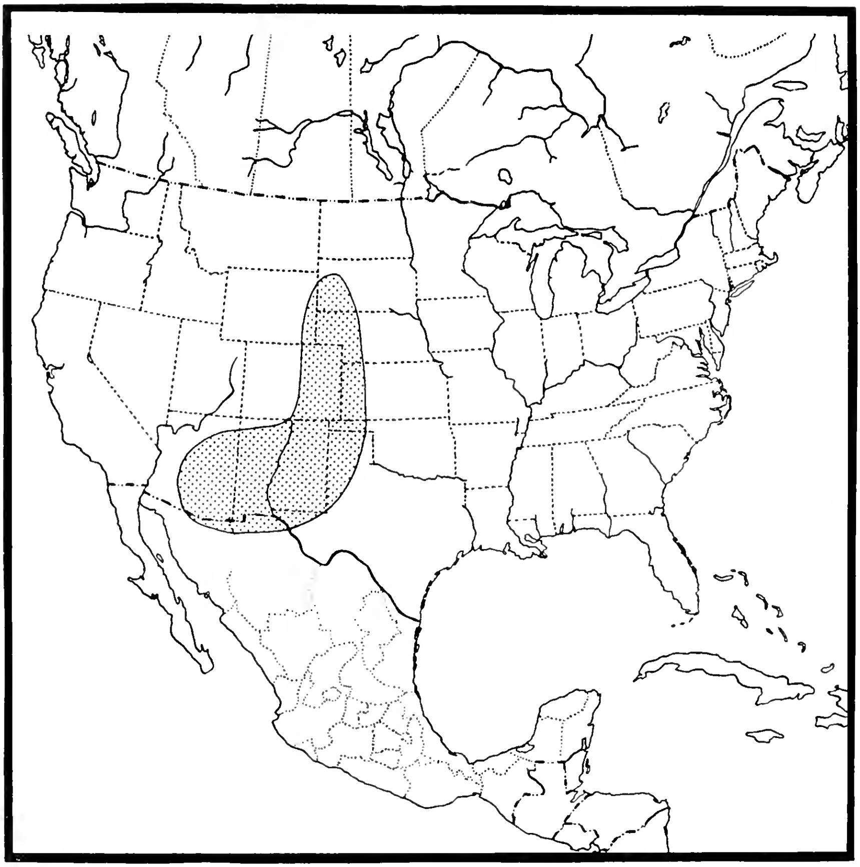

FIG. 28. General distribution of southwestern species which occur within the western half of Kansas and extend north of Kansas in the Great Plains.

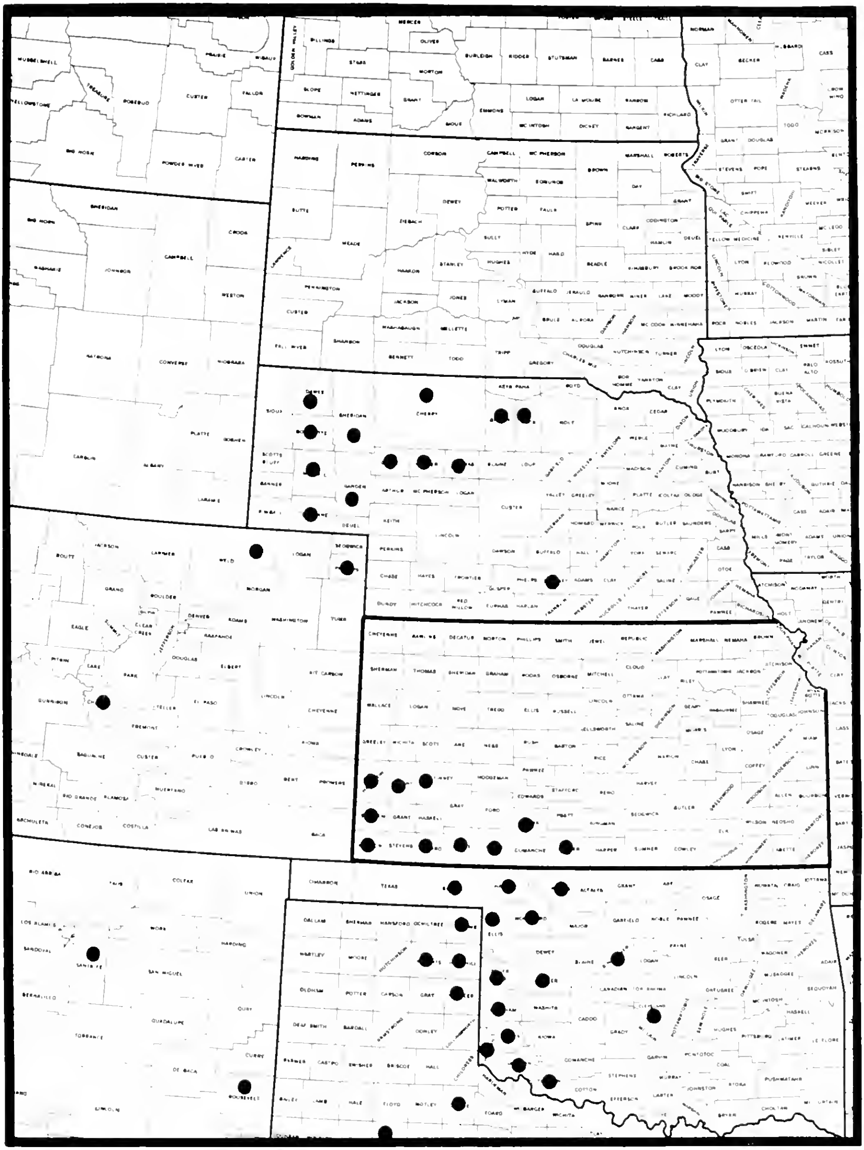

FIG. 29. *Gilia longiflora*

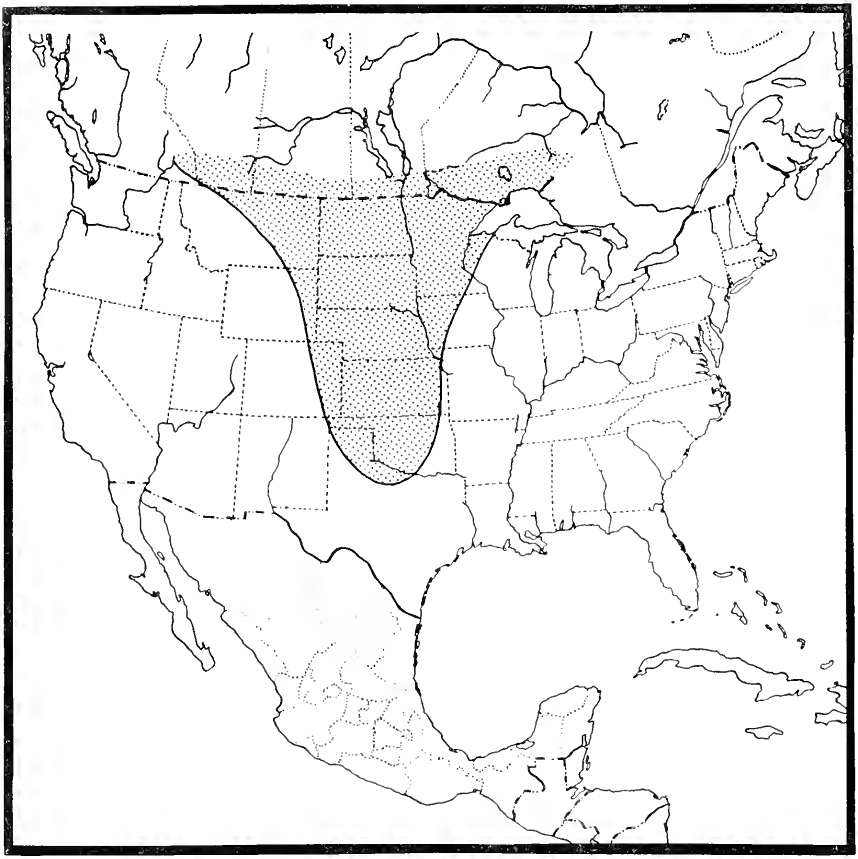

FIG. 30. General distribution of northern species.

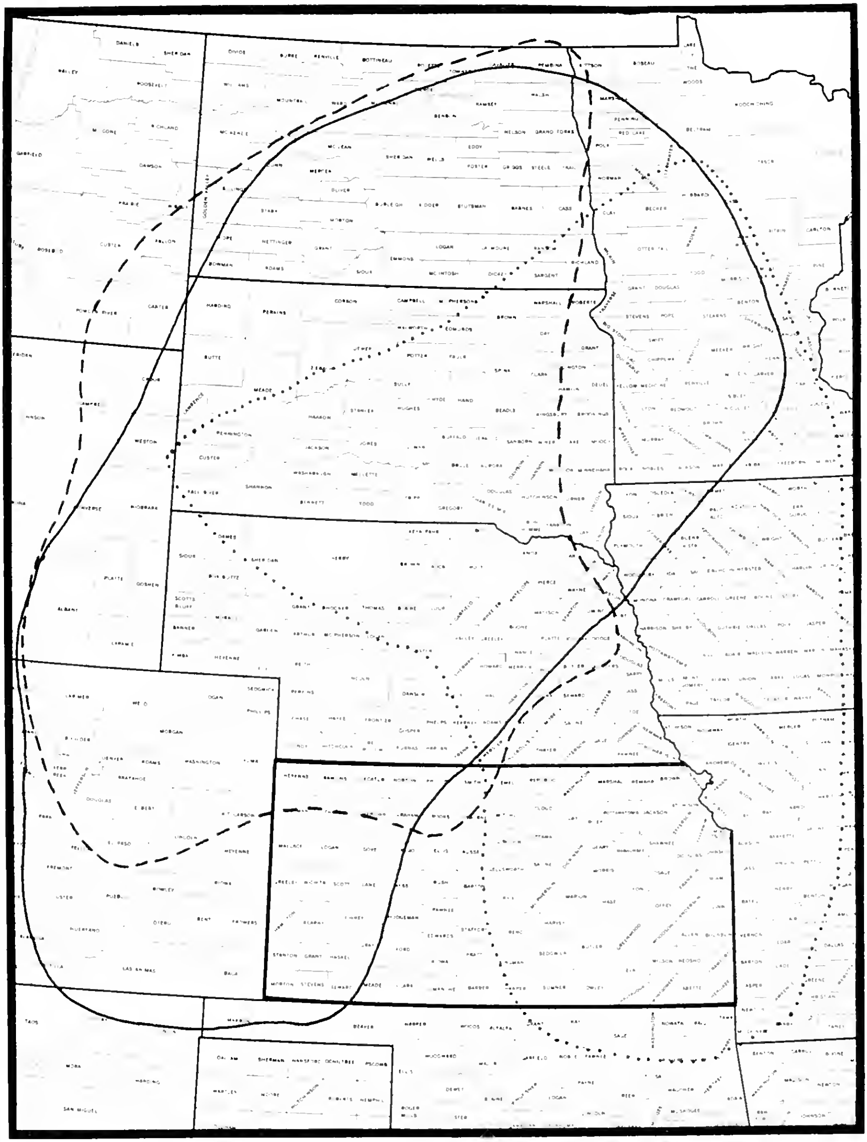

Fig. 31. *Stipa comata* (solid line), *S. spartea* (dotted line) and *S. viridula* (broken line).

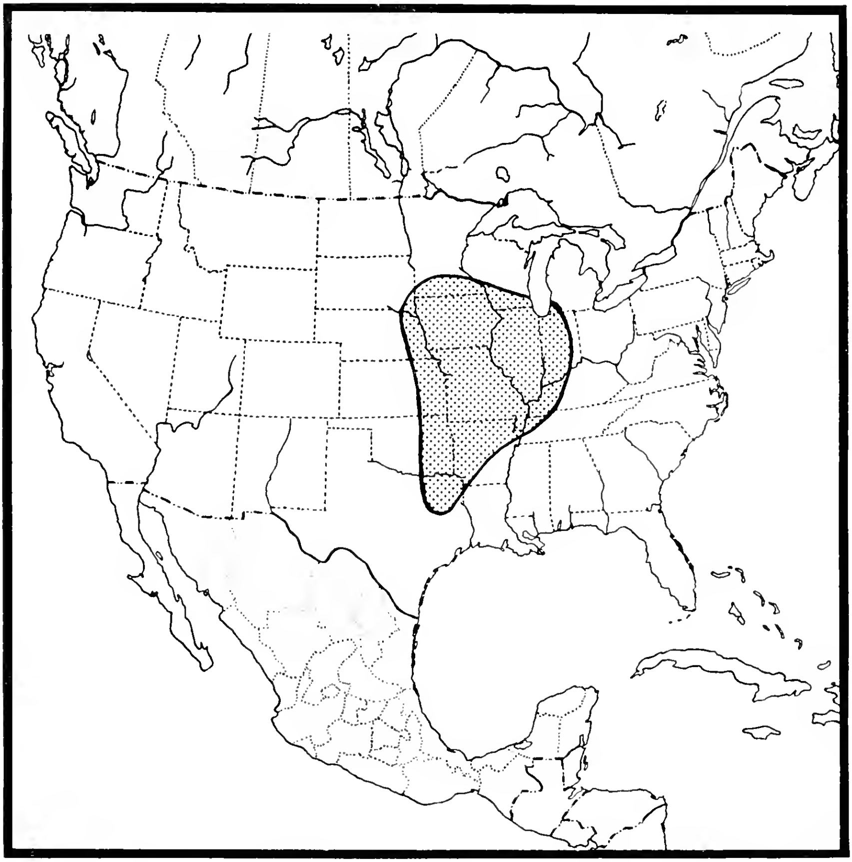

FIG. 32. General distribution of interior species.

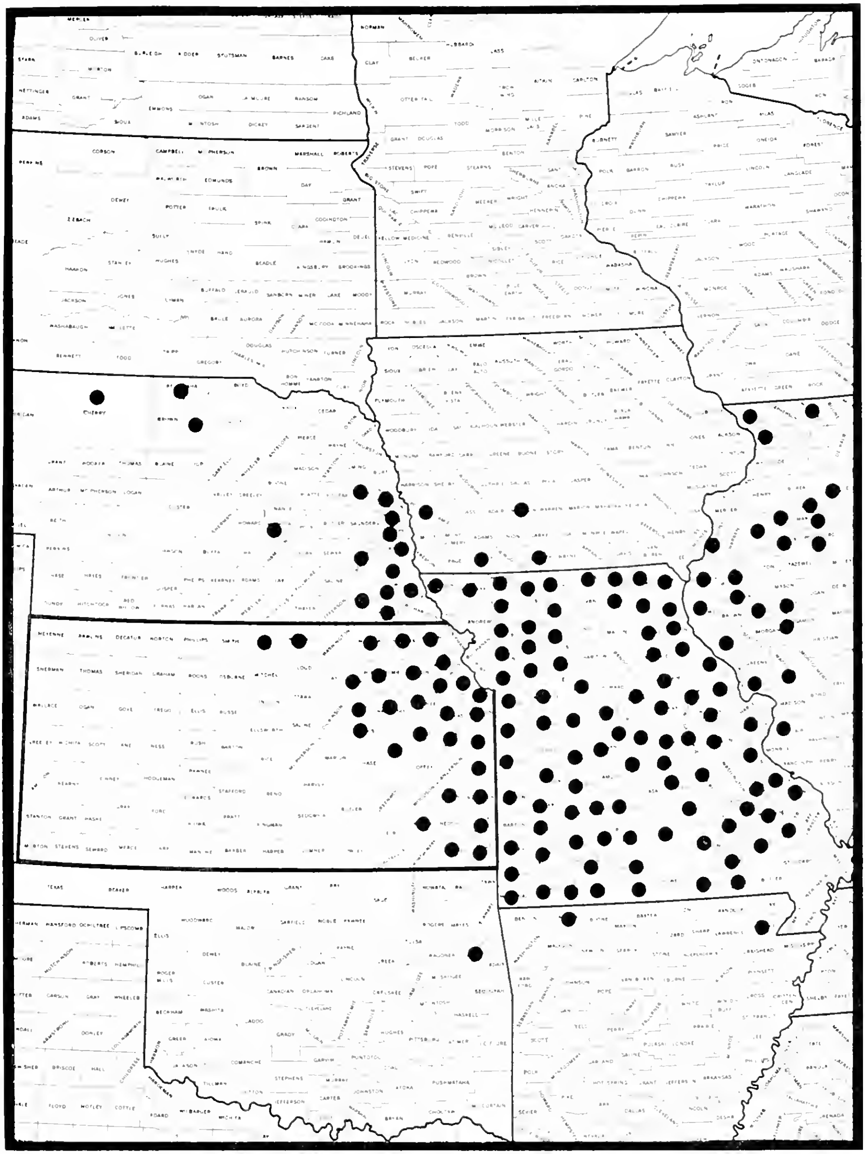

Fig. 33. *Rhamnus lanceolata*

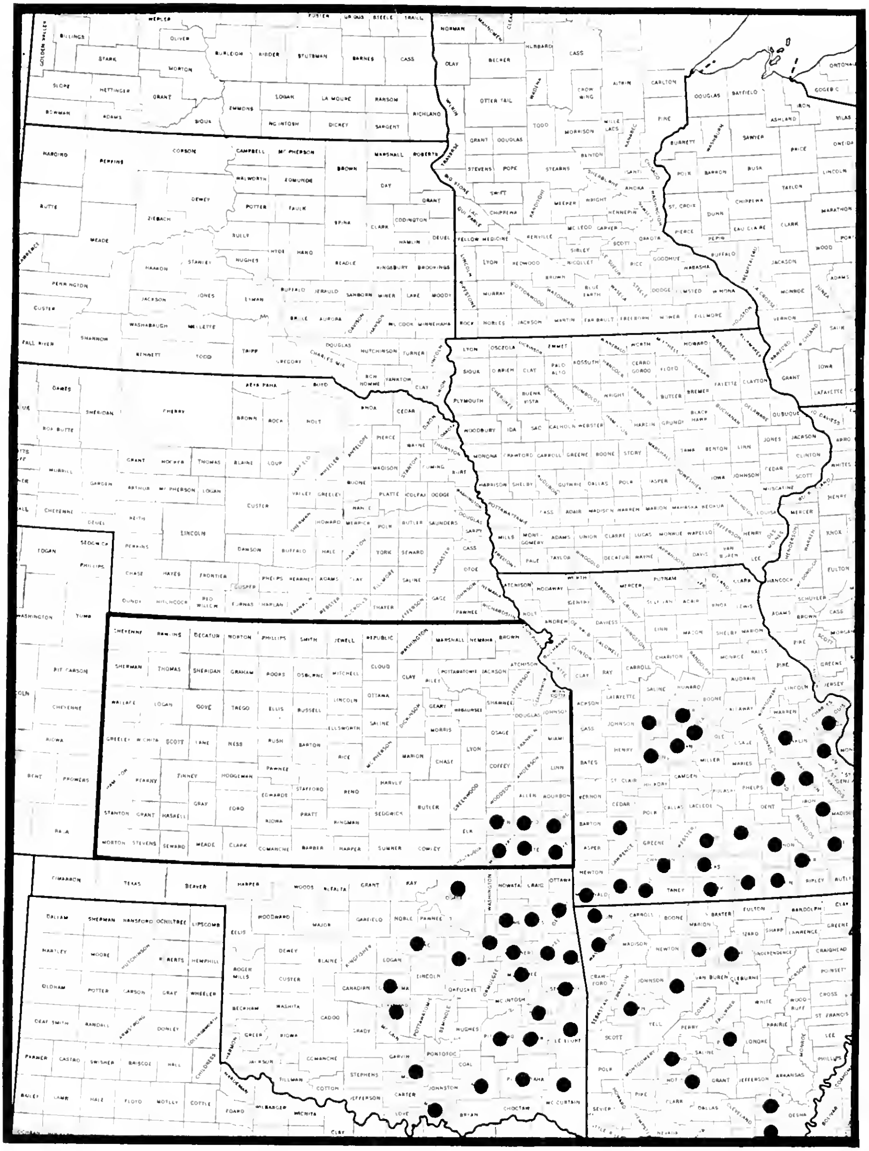

FIG. 34. *Phlox pilosa* var. *ozarkana*

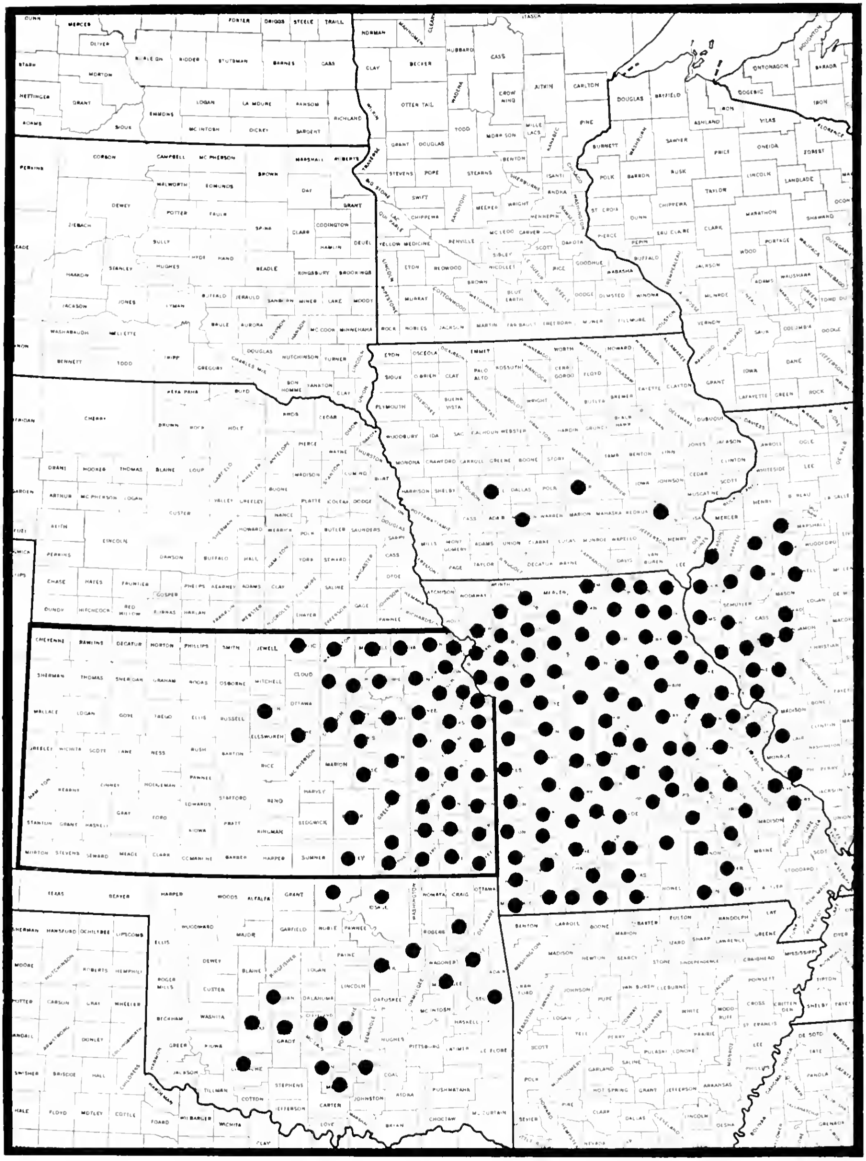

Fig. 35. *Aesculus glabra* var. *arguta*

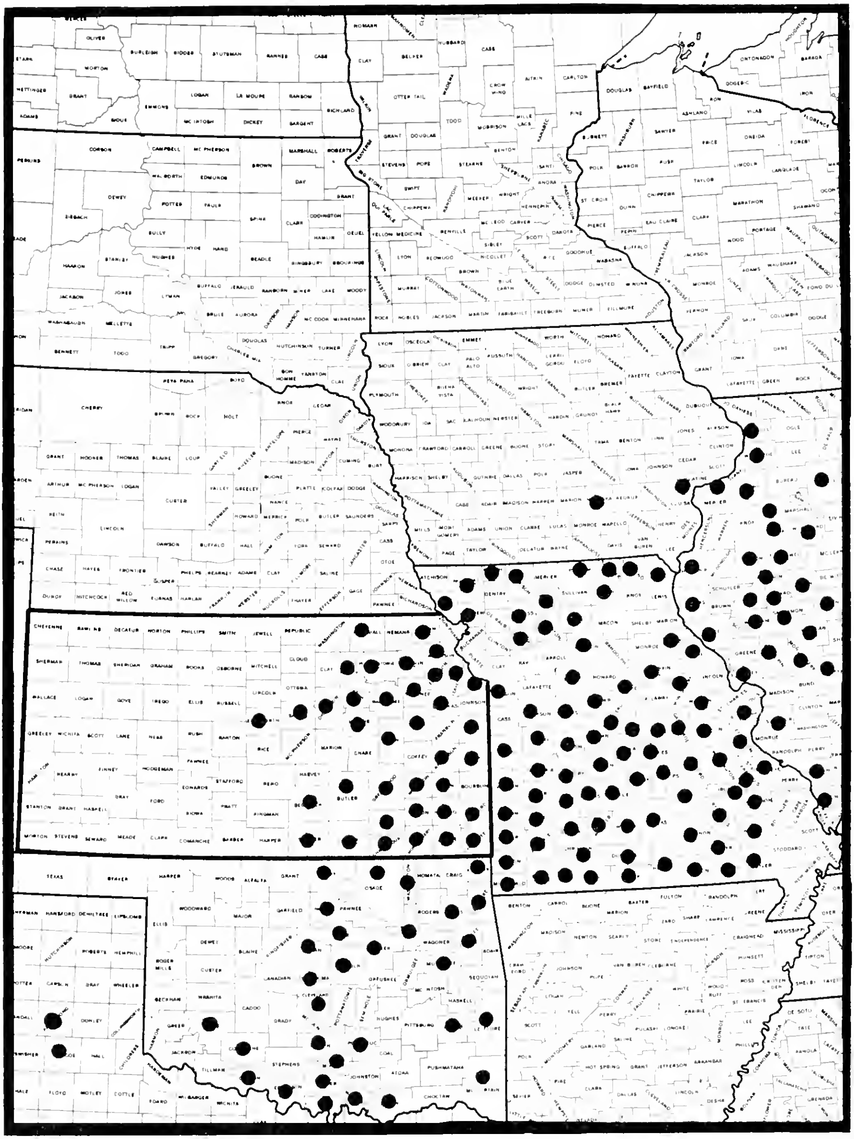

FIG. 36. *Clematis pitcheri*

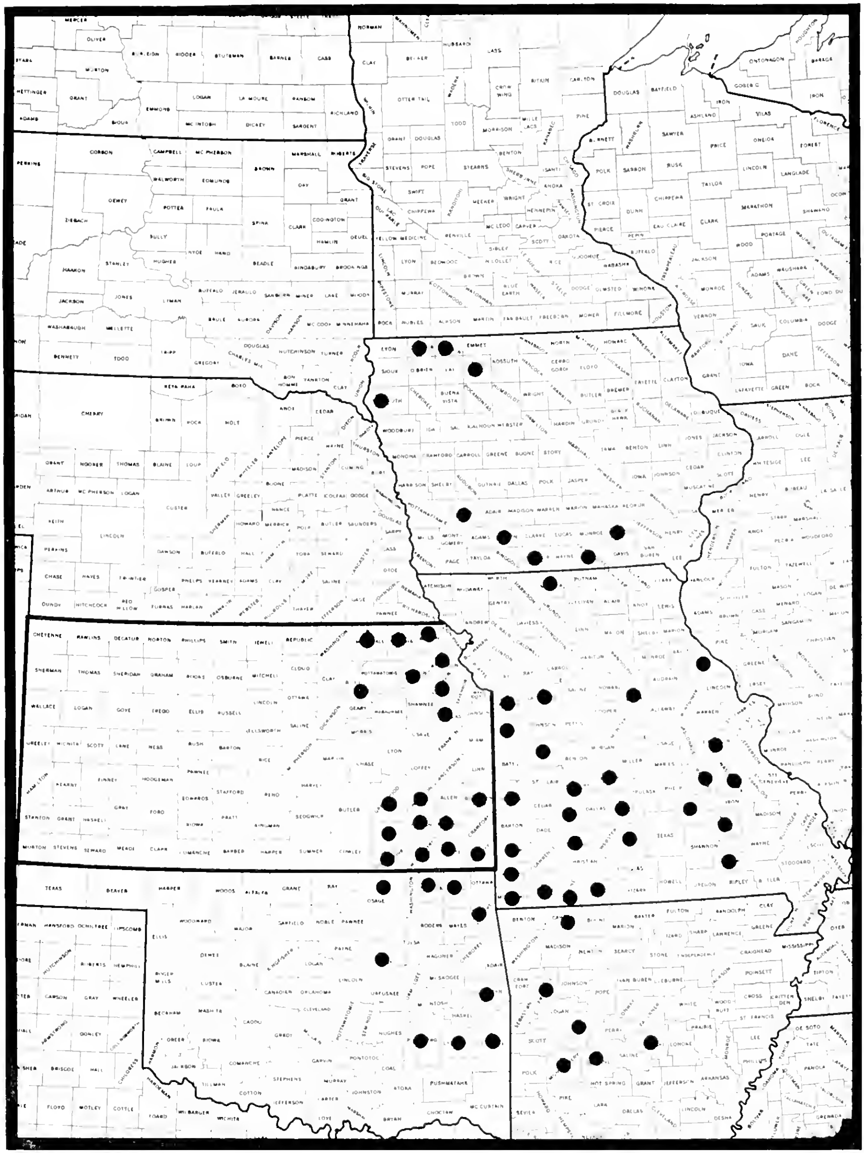

FIG. 37. *Liatris squarrosa* var. *hirsuta*

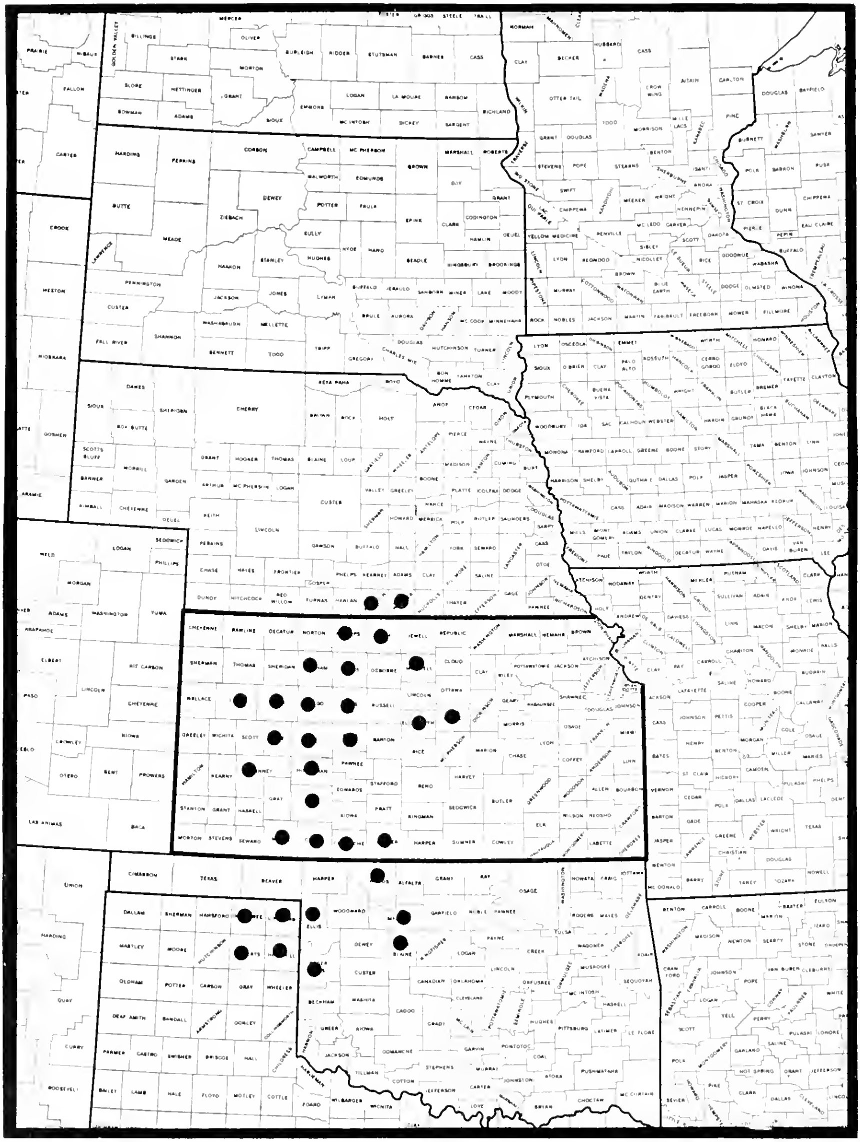

Fig. 38. *Aster fendleri*

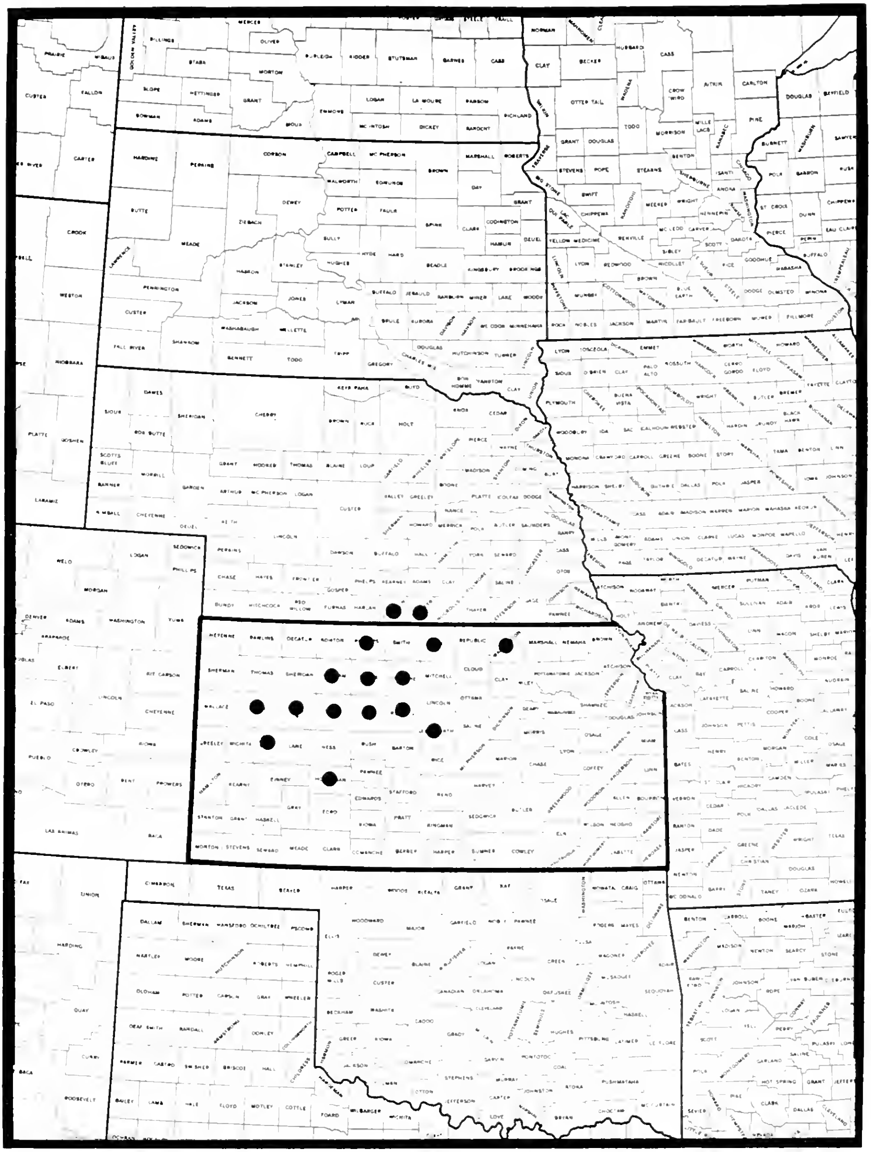

Fig. 39. *Oenothera fremontii*

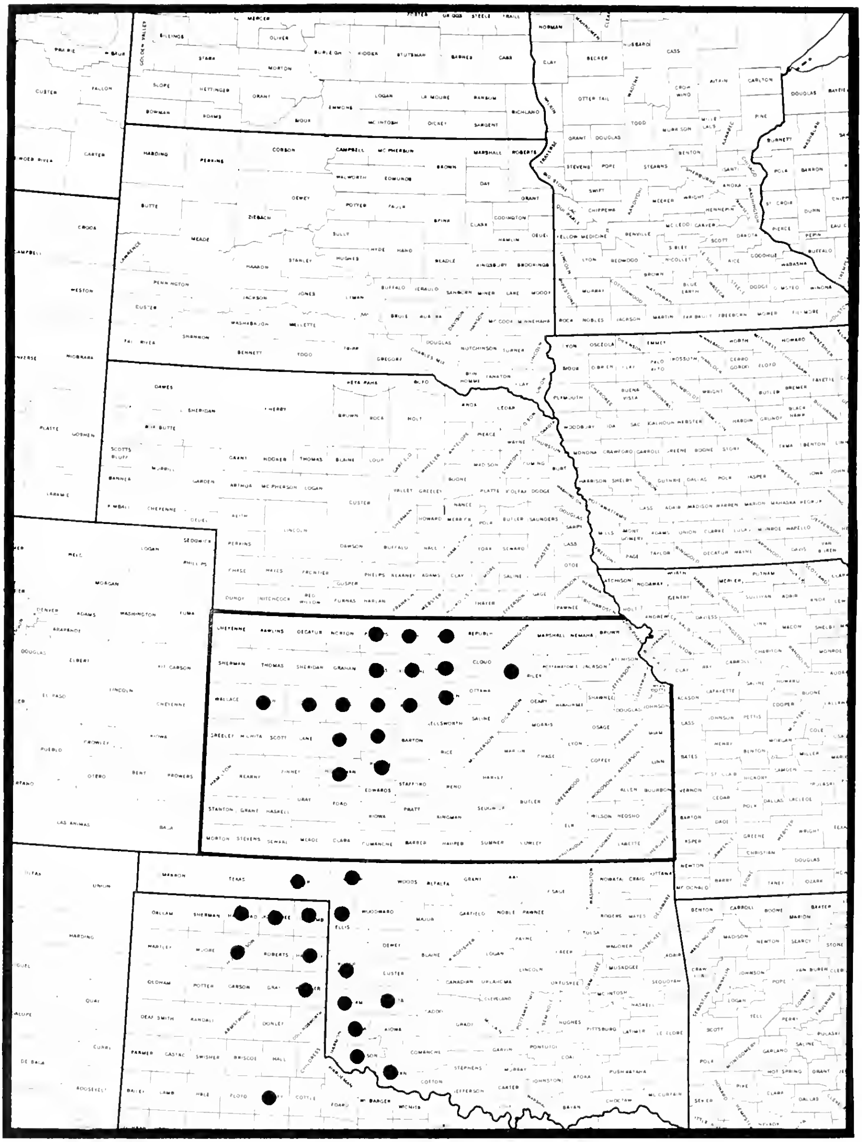

FIG. 40. *Scutellaria resinosa*

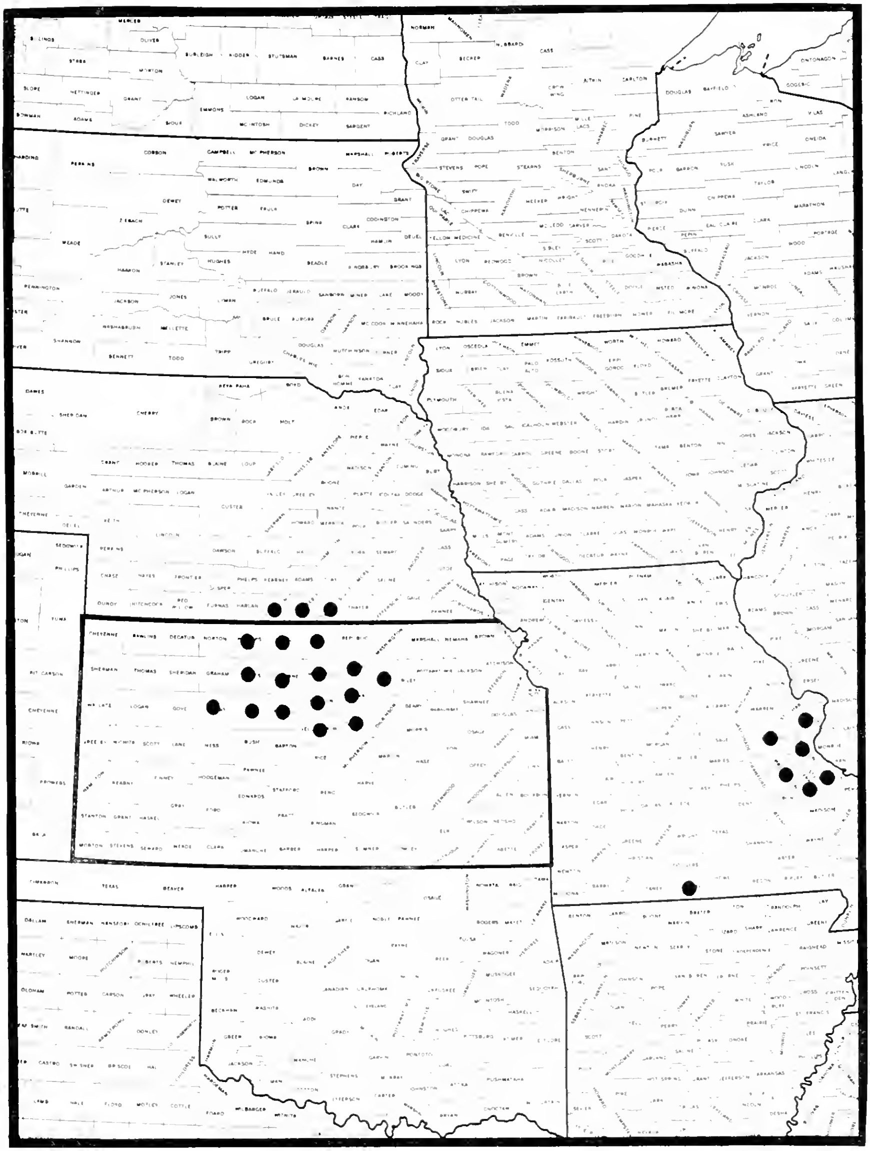

Fig. 41. *Clematis fremontii*

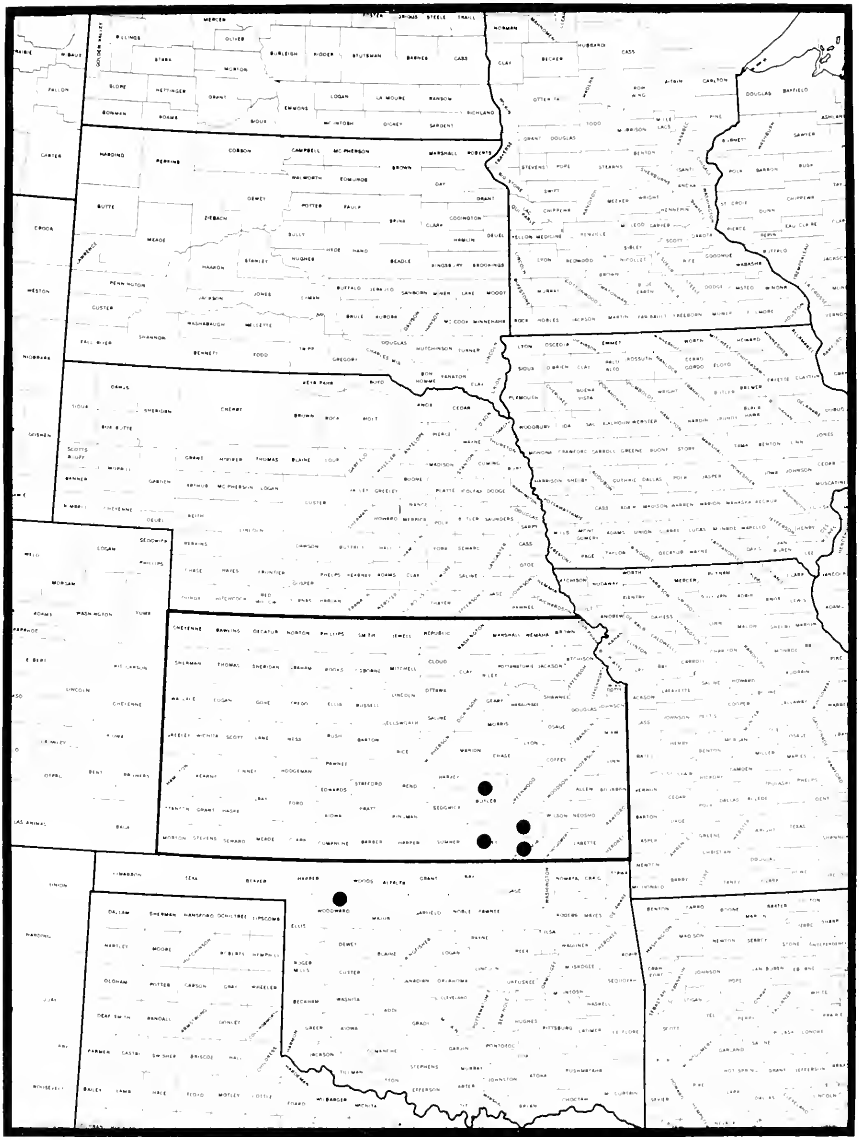

FIG. 42. *Phlox oklahomensis*

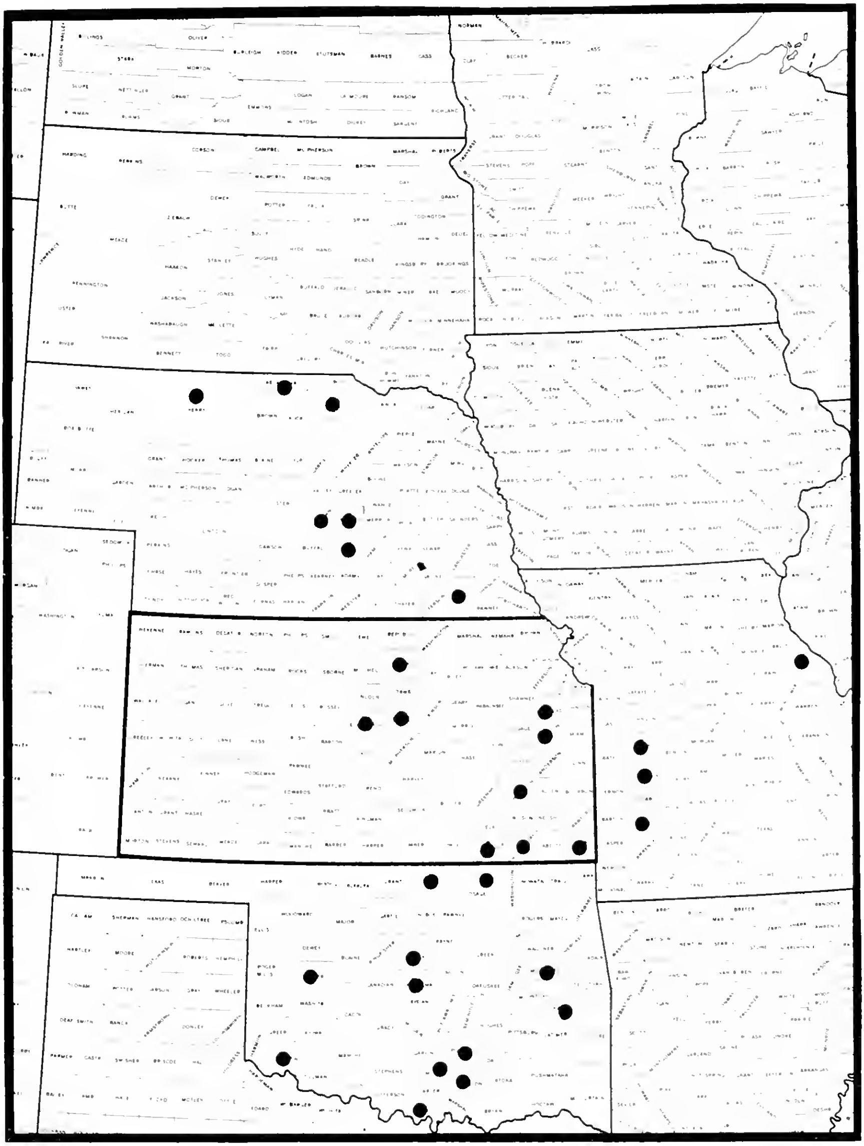

Fig. 43. *Juncus brachyphyllus*

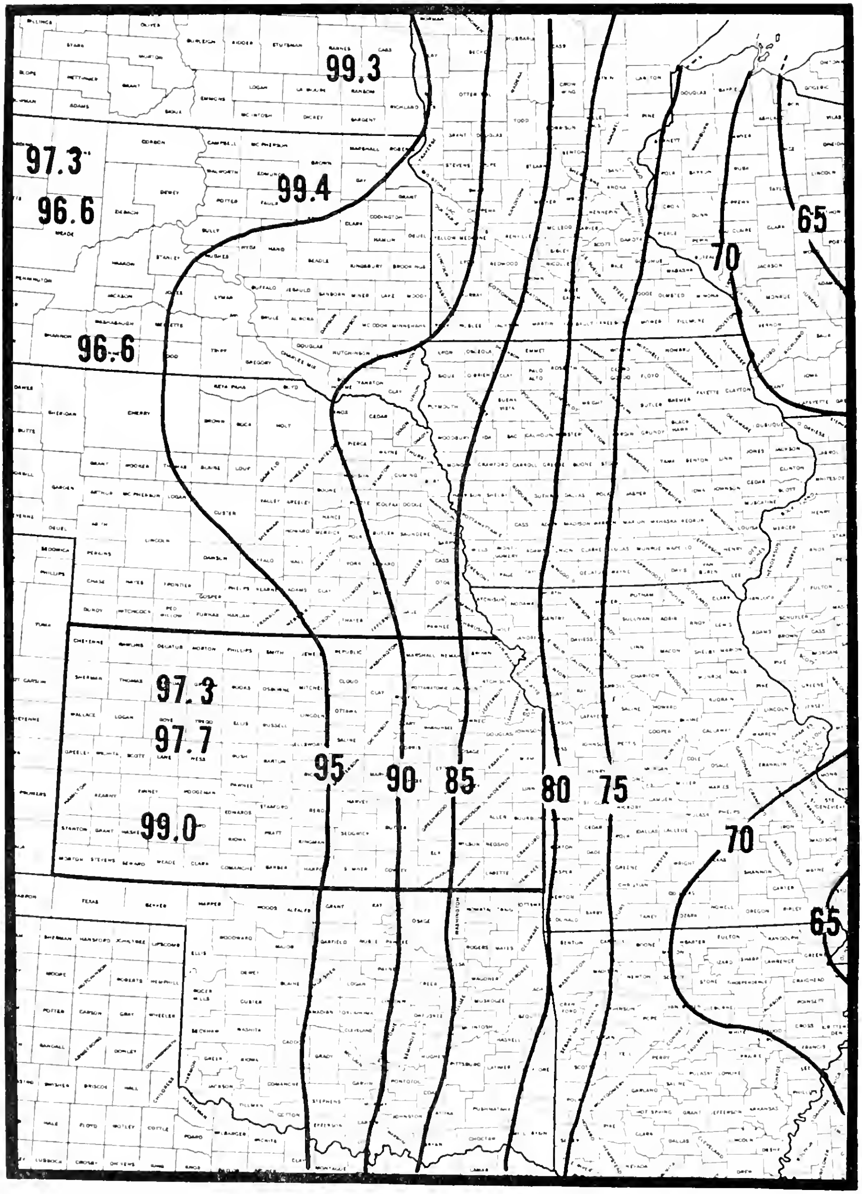

FIG. 44. Mean annual water loss in per cent of rainfall (After Flora, 1948).

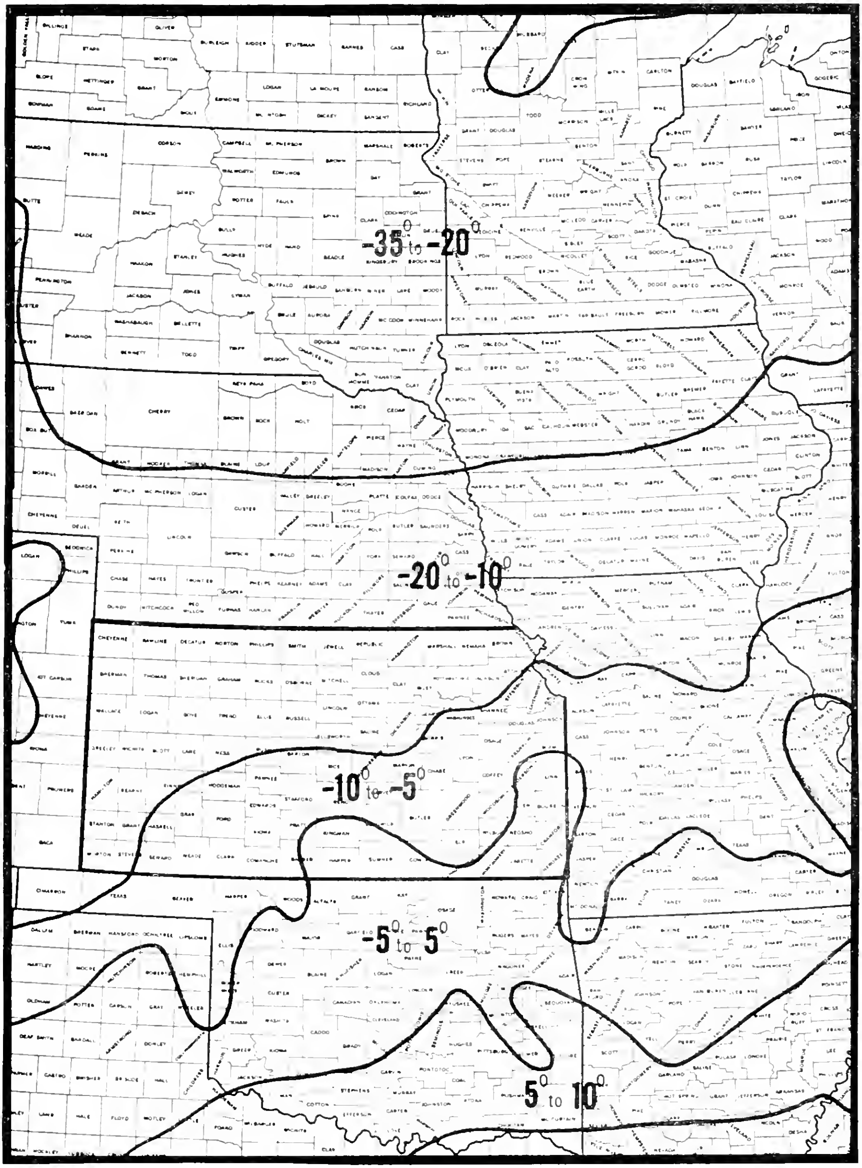

Fig. 45. Plant hardiness zones within the central states (after map by the Arnold Arboretum, 1967). Temperatures are given in degrees Farenheit.