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By Stanley J. Olsen
Florida Geological Survey

With One Plate

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No. 1 — *The Fossil Carnivore* AMPHICYON LONGIRAMUS[1] *from the Thomas Farm Miocene.*

Part II. Postcranial Skeleton

BY STANLEY J. OLSEN
Florida Geological Survey

INTRODUCTION

During the more than a quarter of a century that has elapsed since the discovery of the Thomas Farm deposit (Simpson, 1932), many isolated bones belonging to *Amphicyon longiramus* have been recovered. A sufficient number of skeletal elements of this comparatively rare animal are now known to permit a fairly comprehensive study of the posteranial skeleton of this species of the genus.

Previous workers have described the skeleton of *Amphicyon* as showing a mixture of ursine, feline, and canine characters. However, in no instance have particular details of *Amphicyon* been illustrated or compared with those of other carnivores with which it has been allied. To use such a term as "similar in structure to the bear," without illustrating the element found in the bear, leaves the reader no better informed than he was before picking up the publication. Skeletons of the Florida black bear (*Ursus*[2] *americanus floridanus*, F.G.S. V-5520), the Florida puma (*Felis concolor coryi*, F.G.S. V-5521), and a Walker hound (*Canis familiaris*, F.G.S. V-5775) have been figured and compared with the known elements of *Amphicyon longiramus.* It is hoped that the illustrations will be of value to those readers not having skeletons of the recent forms on hand for comparison. Only those processes requiring special consideration or discussion have been labeled in the drawings.

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[1] Dr. J. A. Wilson has kindly brought to my attention the fact that the specific name *intermedius* White 1940, used by me in Part I of this study, is preoccupied by *intermedius* von Meyer 1849. This species was synonymized by Plieninger (1850) with *Amphicyon eseri.* Since the specific name *longiramus* White 1942 is the next oldest name, it will be used to designate the Thomas Farm species of *Amphicyon.*

[2] There is disagreement among taxonomists as to the generic assignment of this species. Miller and Kellogg (1955) place the black bear in a genus of its own, *Euarctos.*

Since the illustrated bones of *A. longiramus* are most surely not from one individual, it is important to point out that there may be as much as a 13-per cent variation in size between the largest and the smallest specimens of the same element. On making comparisons of bones that articulate with each other, as, for example, the radius and ulna (Figs. 7 and 8), this size difference becomes at once apparent.

The terms "more feline" or "more canine" used in the following pages do not imply that these similarities indicate close taxonomic relationships between these forms and *Amphicyon*. They are in all probability habitus characters.

Only one associated, nearly complete, *Amphicyon* skeleton exists in known collections. This specimen, *Amphicyon* sp. (U.C. 36279), from the Miocene of Colorado, was particularly helpful in determining the foot and vertebral elements of *A. longiramus* among miscellaneous Thomas Farm material.

One other large carnivore, *Aelurodon johnhenryi*, has been described by White (1947) from the same quarry as *A. longiramus*. Specimens of *Aelurodon saevus* (A.M.N.H. 8305) and *Aelurodon haydeni* (U.C. 29638) have enabled me to distinguish the elements of *A. johnhenryi* from those of *A. longiramus*.

Rather than include tables of measurements for the individual bones, a millimeter scale has been included on each plate for ready reference.

The discovery and occurrence of vertebrate remains at the Thomas Farm quarry have been discussed in previous papers, particularly by Olsen (1959) and White (1942).

I wish to thank Dr. R. O. Vernon, Director of the Florida Geological Survey, for permission to undertake this study and for making it possible to do the field work necessary for the collecting of additional specimens. I also wish to express my appreciation to Professors A. S. Romer and Bryan Patterson for allowing me full use of all of the *Amphicyon* material contained in the collections of the Museum of Comparative Zoology, and I am particularly indebted to Professor Patterson for his many discussions and helpful criticisms. Dr. Walter Auffenberg kindly lent me the specimens of *Amphicyon* in the collections of the University of Florida. Doctors R. A. Stirton and D. E. Savage very generously lent me an undescribed, articulated *Amphicyon* skeleton. Doctors G. G. Simpson and W. K. Gregory were particularly kind in answering my inquiries concerning details of the carnivore skeleton with which I was not familiar. Mr. D.

Dwight Davis was particularly helpful in dealing with the structure of the forelimbs in these animals. The figures are the work of Mr. Andrew Janson, scientific artist for the Florida Geological Survey. Outline drawings were made by me from camera lucida projections.

The following abbreviations are used: A.M.N.H., American Museum of Natural History; F.G.S. V-, Florida Geological Survey; M.C.Z., Museum of Comparative Zoology; U.C., University of California; U.F., University of Florida.

URSIDAE

AMPHICYONINAE

AMPHICYON Lartet

AMPHICYON LONGIRAMUS White

Amphicyon intermedius White, 1940, p. 32, pls. 3, 4 (*nec Amphicyon intermedius* von Meyer, 1849, pp. 547-550).

Amphicyon longiramus White, 1942, pp. 6, 7, pl. 5.

Horizon and locality. Lower Miocene, Thomas Farm, Gilchrist County, Florida.

VERTEBRAL COLUMN

(Figs. 1-4)

Cervicals. This series is not represented in the collections from the Thomas Farm quarry.

Thoracics (Fig. 1). The thoracic series is represented by only a single element, the thirteenth vertebra, complete enough for a thorough comparison with the other forms. In general shape and form this vertebra nearly approaches the same bone of *Felis*. This is particularly true of the contour and angle of the neural spine, which is an indicator of the size and proportions of the muscles of the back and to some degree of the extent of action of these muscles.

Hildebrand (1954) in his analysis of the neural spines of the thoracic vertebrae as found in the Canidae observed that these spines are oriented approximately perpendicular to the muscle exerting the greatest strain if several muscles of different strengths are inserted thereon. The spine of the thoracic vertebra of *Amphicyon* indicates a strong development of M. multifidus dorsi, which is inserted on the lower half of the spine, and of M. longissimus dorsi, which is attached (in part) to the distal end of the spine and to the anapophysis. These muscles act as extensors of the back and loins and serve to flex the spine, a most important function in a carnivore running down prey.

The general proportions of the thirteenth thoracic vertebra are similar in *Amphicyon*, *Felis* and *Canis*, all of which differ markedly in this respect from *Ursus*. In the bears, the neural spine is in a more posterior position with relation to the centrum, is nearly perpendicular and lacks a dished edge on the posterior margin of the spine (Fig. 1, U-3). The anapophysis and metapophysis do not terminate in separate peaks in *Ursus*, but are joined instead by a crest or ridge.

The length of the centrum is greater than the width in *Felis*, more nearly equal in the other forms. The ventral surface is keeled in *Felis*, rounded in *Amphicyon*, *Ursus* and *Canis*.

The facet for the capitulum of the rib is deeper and cup-shaped in *Amphicyon*, *Ursus* and *Canis* as compared with the flat depression present in *Felis*.

Lumbars (Fig. 2). The lumbar series is known only from the second vertebra. The anapophysis and transverse processes are incomplete but are preserved in the skeleton of *Amphicyon* sp. (U.C. 36279). This lumbar, like the thirteenth dorsal, exhibits muscle attachments that point to a strong development of MM. longissimus dorsi and multifidus dorsi, indicating well developed extensors and lateral flexors of the back. The metapophyses are not as well developed as those of the other forms. The anapophyses are not as well developed as in *Felis*, having proportions more like those of *Ursus* and *Canis*. The transverse processes have a strong forward deflection almost identical to that seen in *Felis* and are proportionately longer than those of *Canis*. In *Ursus*, these processes are at right angles to the centrum and are shorter proportionately, again not denoting an especially strong extensor musculature of the trunk. The neural spines of the lumbar vertebrae of *Amphicyon* and *Felis* tend to have more of a forward inclination than do these same spines as found in the bear. The centrum has rather similar proportions to those of the bear, and has a keel or ridge on the ventral surface of about the same prominence as in *Ursus*. The faces of the anterior zygapophyses of *Amphicyon* are nearly parallel, as in *Canis*, rather than converging ventrally as in *Ursus* and *Felis*. The dorsal edges of these articular facets terminate in hooklike points, indicating a strong interlocking of this vertebra with its predecessor.

Sacrum (Fig. 3). The sacrum of *Amphicyon* is sturdy in build and possesses a particularly strong area of attachment to the pelvis. The anterior zygapophyses are close to the anteroventral margin of this area in *Amphicyon, Ursus* and *Canis*, rather than standing apart from it as in *Felis*. The neural spines, although broken, have enough of their bases preserved to indicate that they are fused, as in the dog and cat, rather than being widely separated, as in the bear. The sacrum of the bear differs from the other forms in having foramina on the dorsal surface between the bases of the spines. All these forms have large ventral sacral foramina. The anterior zygapophyses of *Amphicyon* have their long axes directed anteroventrally rather than posteroventrally as in the other forms. The posterior zygapophyses are missing in the figured specimen. The ventral keel of *Amphicyon* is flattened, as in the bear and dog in contrast to the definite ridge found in *Felis*. The wings of the attachment for the pelvis project farther ventrally in *Felis* than they do in *Amphicyon, Ursus* and *Canis*. The sacrum of *Canis* is much shorter proportionately than that of the other forms.

The strong fusion of the vertebrae of the sacrum in *Amphicyon, Felis* and *Canis*, is a character in which these forms differ from *Ursus* or the examined specimens of *Lynx rufus*. This may be due to the need for strength in this element to support the strong muscles used in controlling a long tail.

Caudals (Fig. 4). Although the tail of *Amphicyon* is not completely known, enough of the vertebrae are preserved to establish the number as approximately 28, and the length as being nearly that found in *Daphoenodon*.

The neural arch of the seventh caudal is much reduced but the canal is completely arched over, there is no neural spine beyond the twelfth vertebra, the arch fails to enclose the canal and diminishes gradually in each succeeding caudal. The zygapophyses for the first twelve vertebrae are strong and exhibit prominent metapophyses. This condition is not found in the other forms and indicates a proportionately heavier and stronger tail in the Miocene form. The transverse processes are single as far as the seventh caudal, after which they are doubled (at least in the ninth). The ventral tubercles, for the attachment of the chevrons, are well represented although none of these latter elements are known. All of the caudals of *Amphicyon* are keeled on the ventral surface, as in *Felis* and *Canis*. The tail of *Ursus* is hardly more than a vestige, having a total of ten caudals only, and these elements are compressed dorsoventrally and possess none of the features found in the other forms (Fig. 4, U-1 to U-6). The tail of *Felis* contains 21 elements, that of *Canis* 19.

The structure of the tail is in general unlike those of the modern forms with which it has been compared, being more like that of the Miocene *Daphoenodon*.

RIBS AND XIPHISTERNUM
(Fig. 5)

The ribs of *Amphicyon longiramus* are poorly preserved; no complete one is known. Well preserved proximal ends of the right third rib and the left eleventh rib are here used for the brief description of these not too diagnostic elements.

The head and tubercle of the third rib are nearly alike in *Amphicyon* and *Ursus*. In both animals the tubercle has a decided downward deflection when compared with the long axis of the rib, whereas in *Felis* and *Canis* it is more at right angles with the main body of the rib. The eleventh rib is also nearly identical with that of *Ursus* and, as in that form, has a more pronounced tubercle than in *Felis* and *Canis*. The head is smaller in *Canis* than in the others.

The xiphisternum is known from one specimen (Fig. 5, A-7 to A-9). The stoutness of this element in *Amphicyon* and, in particular, the strong keel, suggests that the sternum as a whole was well developed in this animal.

SCAPULA
(Fig. 6)

The scapula of *Amphicyon* has a large postscapular fossa lying caudad to the infraspinous fossa on the axillary border, as in the bears, and it is separated from the infraspinous by an inferior scapular spine (Fig. 6, A-1). The postscapular fossa is well developed in all bears, regardless of size, and is also present in the Procyonidae. This fossa is wanting in the Canidae and the catlike carnivores, but is present in many of the early doglike carnivores.

The scapula in *Amphicyon* and the bear is rectangular in outline, instead of being fan-shaped as in the puma and dog. The neck is much heavier in *Amphicyon* and *Ursus*. The acromion is heavy and shelflike with no noticeable metacromion process for M. levator scapulae ventralis, such as is present in the puma (Fig. 6, F-1). There is a large nutrient foramen at the base of the acromion process of *Amphicyon* (M.C.Z. 24419), directed at a right angle to the long axis of the blade, to carry the blood vessels and nerves which innervate the muscles occupying the postscapular fossa. A similar foramen is not found in the other forms. The acromion process in *Amphicyon* projects beyond the glenoid fossa to the same degree as that of *Ursus*.

The coracoid process of *Felis* has a projecting point at its terminus which is unlike anything found in the other compared forms (Fig. 6, F-2). The dog has a well developed scar for M. teres major (Fig. 6, C-1) that should not be confused with the postscapular fossa found in the bear and *Amphicyon*.

The postscapular fossa is occupied by the subscapularis minor, the teres major, and the posterior head of the triceps longus muscles. Davis (1949, p. 298) points out that many of these short powerful muscles in the scapular region are far more important in fixing the joint than in producing movement. This is particularly true of the subscapularis muscle. The need for this strong fixing of the shoulder is not at all clear in the case of *Amphicyon*. If the development of these muscles were an aid in holding down prey, a similar development would be evident in the lion or hyena, which is not the case. Bears are powerful climbers, using a bracing action in climbing. When the hind limbs move up for a new hold, the forelimbs support the weight of the body, so that an unusually strong forelimb musculature is necessary. Whether this type of action was indulged in by *Amphicyon* cannot be proven from the skeleton alone, but it can be said that the shoulder architecture is closer to that of the bear than to that of any other form with which it has been compared.

FORELIMB
(Figs. 7-12)

Humerus (Fig. 7). Two features of the humerus of *Amphicyon* are strikingly apparent. These are the entepicondylar foramen and the unusually long ridge of the deltoid crest.

The entepicondylar foramen is characteristic of the felids among the living carnivores. However, it is present in the humerus of many carnivores other than cats (i.e., *Borophagus, Aelurodon* and *Daphoenodon*), and is also found in the Pleistocene bear *Arctotherium* (Merriam and Stock, 1925). This large opening has attracted relatively little attention among students of mammals but is discussed in some detail for reptiles by Romer and Price (1940, p. 140) and by Romer (1956, p. 353). These authors state that the entepicondylar foramen appears to be associated with a strong development of the extensor musculature and that loss is related to a reduction in size of the entepicondyle as a whole. W. K. Gregory (personal communication) suggests that development of this area may be an indication of a crouching habit with strongly flexed elbows as the entepicondylar foramen is not present in the large ungulates with pillarlike striding limbs. However, Professor Patterson (personal communication) points out that it is present in large pantodonts. Landry (1958) suggests that the entepicondylar foramen acts as a retinaculum for the median nerve, to prevent it from slumping across the angle of the elbow. He further states that graviportal mammals have lost the entepicondylar foramen because they do not abduct the humerus and thus do not expose the median nerve. D. D. Davis (personal communication) has observed that this foramen transmits the median nerve and may or may not transmit the brachial artery and that both of these structures are laid down in the embryo before the bone is definitely organized. That this opening is a fairly constant character, in some extinct forms, is indicated by the findings of Merriam and Stock (1932, p. 114) in their study of the Felidae from Rancho La Brea. In a series of 238 humeri of *Smilodon*, only one specimen lacked the entepicondylar foramen. It is present in all seven known specimens of *Amphicyon longiramus*. The bear has a proportionately larger development of the medial epicondyle than the puma but lacks the entepicondylar foramen present in the latter. The flexor muscles of the lower limb, and those that control the flexing and pronation of the forepaw, are attached to the medial epicondyle. The size of this process in the bear and *Amphicyon* suggests a stronger musculature in this area than that occurring in the puma and dog.

The lateral supracondyloid ridge is of nearly the same proportions in *Amphicyon* and the bear, and is much less developed in the other two forms. The extensors of the forepaw have their origin on this ridge and, as in the case of the medial epicondyle, their size suggests a stronger extensor musculature in *Amphicyon* and *Ursus*. The deltoid crest is of nearly equal prominence in *Amphicyon* and *Ursus*, extending over approximately two-thirds the length of the shaft. Judging by the processes of the humerus and scapula, the muscles of the bear and *Amphicyon* were of nearly the same proportionate size and bulk, performing the same function in both forms.

The coronoid and olecranon fossae often communicate through a large supratrochlear foramen in the dog (Fig. 7, C-1). This is not true of the other three forms.

It does not appear on the evidence presented that the size of the medial epicondyle has a direct bearing on whether or not the entepicondylar foramen is present or absent, or that this foramen indicates a particularly strong muscle development of the forelimb.

Radius (Fig. 8). The head of the radius has a distinct raised peak on the anterior margin of the capitular depression in both *Amphicyon* and *Ursus.* This peak is situated at the point of articulation of the radius with that of the junction of the capitulum and trochlea of the humerus. This same surface in *Felis* and *Canis* is more cup-shaped, with little or no raised area present. Between the styloid process and the ulnar notch is a raised area in which there is a groove for M. extensor carpi radialis brevis, a muscle which extends the wrist and may act as an abductor of the forepaw. This raised area is nearly the same in the bear and *Amphicyon*, much more pronounced and isolated in the puma, and almost lacking in the dog. The styloid process is directed in nearly the same ventral plane in *Amphicyon* as in the bear and the dog, but is inclined in a more medial plane in the puma. The proximal flaring of the styloid process is quite distinct in *Amphicyon* and the puma, but is nearly absent in the other two forms. The radial tuberosity, on which is inserted M. biceps brachii, and the scar for M. pronator quadratus just below it are quite rugose and occupy a proportionately larger area in *Amphicyon* than they do in the other animals; the scar for the latter muscle in *Ursus* is the closest to *Amphicyon* of these compared forms. These muscles aid in the control of the flexing of the forearm and the pronation of the forepaw and, as suggested by the size of the attachments, were quite strong in *Amphicyon.* The heads of all forms examined, excepting *Canis*, have a medial deflection. In *Canis*, the plane of the articular depression is nearly at a right angle to the main axis of the radial shaft. The articular surface for the scapho-lunar in *Amphicyon* resembles that of the bear more closely than it does any of the others. The ulnar notch is well defined and very similar in all.

Ulna (Fig. 9). The superior surface of the olecranon in all compared forms has a roughened area for the attachment of M. triceps brachii, the great extensor muscle of the forearm. In all except the bear, the front of this process exhibits a groove for the attachment of the posterior ligament of the elbow joint. In the bear, this surface is marked by a rounded crest with a pitted lateral face for the attachment of the ligament. The posterior portion of the olecranon is plainly deflected toward the radial side in *Amphicyon*, the bear and dog, but not to nearly the same degree in the puma. The apex of the coronoid process is directed outward in *Amphicyon*, the bear and dog, but has a downward deflection in the puma. The radial notch of the dog has little or no lip setting it off from the surface of the ulnar shaft as is found in the others. The semilunar notch has about the same degree of twist and surface for articulation in *Amphicyon* and the bear, indicating a better locking mechanism between this bone and the humerus in these two forms than in the dog and puma. The interosseous crest, although well developed in all four animals, is rather more rugose in *Amphicyon* and *Felis*. The styloid processes of *Amphicyon* and *Ursus* are of nearly the same form, and both have a hooklike termination at the point of articulation with the carpus. In *Felis* the styloid process lies in a nearly straight line with the long axis of the ulnar shaft and has a strong articular surface. The styloid process of *Canis* is merely a rounding of the distal end of the shaft.

Forefoot. The carpals are poorly known, being represented only by the scapho-lunar (Fig.10). This bone, although showing some resemblance in general shape to that of the puma, is unlike that of any of the other forms. The facet for the radius is a broadly rounded surface in all forms; *Amphicyon* and the puma have a ridge at the junction of this surface with that of the tubercle. The surface for articulation with the trapezoid is shallow in the bear, deep or cup-shaped in the other three forms. The articular surface for the magnum is well defined in all except the puma, in which it is merely a shallow groove.

The metacarpals and phalanges are also poorly known, and are represented only by the elements of the third digit (Fig. 11). Almost certainly the manus consisted of five digits with the third the longest as in *Daphoenodon*. In general form, metacarpal III of *Amphicyon* is almost indistinguishable from that of *Ursus;* the facets for the carpals and neighboring metacarpals are of nearly the same form and proportions in both animals. In *Felis* the articular area for metacarpal II consists of two separate facets, whereas in *Amphicyon*, the bear, and the dog this face is one continuous articular arc. When viewed from the side, the metacarpals of *Amphicyon*, *Ursus* and *Felis* all present an arched curve, that of *Felis* being longer and more slender in build. The same element in *Canis* is nearly straight and has a much more rounded proximal articular surface.

The proximal phalanges of digit III are of nearly the same proportions in *Amphicyon*, the bear, and the dog. In the puma the median phalanx is asymmetrical, due to a recess for the retractile claw, and a quite distinct tendinal scar is present on the palmar surface of the proximal end (Fig. 11, F-6). This scar seems to be present only in those forms having fully retractile claws; it does not occur in *Amphicyon*, the bear, or the dog.

The *ungual phalanx* (Fig. 12) in *Amphicyon* and *Ursus* is nearly the same, having a well developed hood and a blunt ungual process with little or no curve (Fig. 12, A-1 and U-1). In *Felis*, the subungual process on the lower articular surface is set at an angle (Fig. 12, F-2) to facilitate the entry of the ungual phalanx into the recessed surface of the middle phalanx (Fig. 11, F-6). This articular margin is nearly straight in the other forms. In *Felis*, the palmar surface of the ungual process is set at more of an angle in relation to the articular surface than it is in the other forms and indicates the greater retractibility of the claws in this animal (Fig. 12, F-1).

Although some previous writers (Peterson, 1910; Scott and Jepsen, 1936) have described the claws of *Daphoenodon* and *Daphoenus* (nearly identical to those of *Amphicyon*) as being capable of "partial retraction." this term has little or no meaning, since all carnivores can, of course, control the movement of their claws to some degree. It seems that such descriptions have been used to bolster a hypothesis of relationship based on the few other "catlike" features of the skeleton. However, on the evidence of the bones, and particularly on that of the muscle scars, such a conception of relationships is untenable. The claws of *Amphicyon* were almost certainly movable to the same extent as and no more than those of the bear and in all probability were used in much the same manner.

INNOMINATE
(Fig. 13)

The innominate is known from two incomplete specimens, in both of which the descending ramus of the pubis is missing. On comparing the innominate of *Amphicyon* with those of the other three carnivores, it is apparent that although this element more nearly resembles that of the bear in shape and form it is unlike *Ursus* in several details. The neck of the ilium is particularly short and thick in *Amphicyon* and the bear, and less constricted than in the other two carnivores. The iliac crest does not flare outward as it does in the bear and dog, nor is it nearly as restricted at the terminal end as it is in the puma. The lateral face of this crest is better developed in *Amphicyon*, the bear and the dog than in the puma. The ischiatic spine is well developed in *Felis*, smaller in *Amphicyon* and *Canis*, and nearly lacking in *Ursus*. The prominence of this area is correlated with the size of MM. gemellus, biceps femoris, and semitendinosus, which have their origins at this point on the pelvis. Their function is to rotate the femur outward and to extend the hip joint. The iliopectineal eminence and the tubercle for M. rectus femoris are well defined in all forms. MM. psoas minor and rectus femoris flex and incline the pelvis and loins in a lateral direction and flex the hip joint. The tubercles for the attachment of the latter muscles are particularly well developed in *Amphicyon* and *Ursus*, possibly due to a strong development of these muscles as an aid in ''prop'' climbing. The obturator foramen is nearly round in all forms except *Felis*, in which it is oval-shaped with the long axis directed anteroposteriorly. Proportionately, the acetabulum is smallest in *Felis* and the articular surface of this socket greatest in *Ursus*.

HIND LIMB
(Figs. 14 to 21)

Femur (Fig. 14). The shafts of the femora of *Amphicyon* and *Felis* tend to be straight when viewed from the side, as contrasted with the curved profile of *Ursus* and *Canis*. Hildebrand (1954) and Howell (1930), in their discussions of this feature of the mammalian femur, do not give any reasons for this variation in curvature, the latter commenting only that it is not a function of posture. The significance of the straightening of the femur in *Amphicyon* and *Felis* is not clear. The most obvious difference in the four animals examined is the degree to which the femoral head extends above the greater trochanter, this being greatest in the bear (Fig. 14, U-1). The heads of the femora of *Amphicyon*, *Felis* and *Canis* are similar in proportions and extend out from the shafts to about the same degree. The greater trochanter of *Ursus* is relatively small. M. gluteus medius is inserted on the greater trochanter and acts to extend and abduct the hip joint; this action is perhaps weaker in *Ursus* than in others. The scar for M. vastus medialis, which controls the extension of the knee joint, is most prominent in *Felis*. This is in all probability due to the more powerful and flexible nature of this joint in a springing form such as the puma. The lesser tuberosity is about the same proportionate size in all forms except the bear, in which, although plainly visible, it does not rise to a peak as it does in *Amphicyon*, *Felis* and *Canis*. The fovea capitis femoris is deeper in *Amphicyon* and *Ursus*. The neck has a more pronounced lip or overhang at its junction with the head in *Felis* and *Amphicyon* as compared with the more gentle blending of these two surfaces in *Ursus* and *Canis*. The distal end of the femur of *Amphicyon* resembles that of *Felis* in general contour, having well developed, rugose epicondyles, which are not found in *Ursus* and *Canis*. The patellar surfaces, condyles, and intercondyloid fossae are well developed in all these forms and have no features distinguishing them.

Tibia (Fig. 15). The tibia of *Amphicyon* resembles that of the felids in general shape and proportions; it shares a few characteristics with the bear and is quite different from that of the dog. In *Ursus* this bone is proportionately shorter and more massive, in *Canis* lighter in build and with a decided curve (Fig. 15, C-1). All these forms have well defined crests, those of *Amphicyon* and *Ursus* being more rugose than those of *Felis* and *Canis*. The crest of the latter differs from those of the others in having a decided angle at its distal extremity. The portion of M. biceps femoris that flexes the knee attaches to this crest. Judging by the relative size of the crest in *Amphicyon* and *Ursus*, this action would appear to be stronger in these animals than in *Felis* or *Canis*. The posterior face of the shaft, immediately below the condyles, presents a grooved surface for the insertion of M. popliteus and is grooved laterally for the origins of the posterior tibial, flexor digitorum longus, and flexor hallucis longus muscles which rotate the thigh and extend the foot and phalanges. The muscle scars in this area of the tibia of *Amphicyon* indicate that these muscles were particularly well developed in this animal. This is also true of *Felis* but not of *Ursus* and *Canis* to anything like the same degree. The medial malleolus of *Amphicyon* is proportionately longer than in the others, but the groove for the tendon of the flexor digitorum longus muscle is not as deep as that found in *Felis*, being more like that of *Ursus*. The notch for articulation with the fibula, situated opposite the medial malleolus, presents a strong surface for attachment in *Amphicyon* but is not as concave as that of *Felis*. This last statement applies to *Ursus* and *Canis*, as well as to *Amphicyon*.

Fibula (Fig. 16). The fibula is quite heavy with well developed tibial facets. The shaft is roughly triangular in cross-section and has strong ridges for the attachment of muscles. The tendon of the fibularis longus passes through a groove in the lateral malleolus. The depth and size of this groove suggest a powerful development of the muscles and thus a well developed capability for flexing the tarsus and turning the plantar surface of the paw. The fibula of *Amphicyon* is unlike any of the compared forms; it has neither the hammer-shaped head (Fig. 16, F-1) of the puma nor the club-shaped head of the bear and the dog (Fig. 16, U-2, C-2).

Hind Foot. Enough elements of the hind foot of *Amphicyon* have been collected to permit the assembling of a composite tarsus (F. G. S. V-5774), in which only the mesocuneiform is unrepresented (Fig. 17). The hind foot in *Amphicyon*, as in *Ursus*, has five well developed digits. In general proportions and build the foot resembles that of the bear rather than that of the puma or dog. It is true that when the feet of *Daphoenodon* (or *Amphicyon*) are compared only with the dog and cat the foot bones are found to be ''more feline than canine'' (Peterson, 1910, p. 238), but when an ursid foot is added to the comparative material the similarity to the felines is seen to be less than to the bear.

Whether or not *Amphicyon* can be called truly plantigrade is open to argument, as is the case with the present-day bears. Raven (1936) claims that the gait of the bear is not truly plantigrade because the heel and the proximal part of the foot is kept off the ground while walking. On the other hand, in a recent work by Davis (1958) dealing with the tarsal ligaments of the spectacled bear, ursids are referred to as plantigrade walkers. It is difficult, as regards *Amphicyon*, to settle this question on skeletal evidence alone.

The astragalus of *Amphicyon* (Fig. 18) is represented by 12 specimens. In general proportions, this bone approaches that of *Felis*, differing particularly from that of *Ursus* in that the process supporting the facets for the calcaneum and navicular (Fig. 18, A-1 and A-4) is proportionately much longer than in the bear. The articular surfaces in *Felis*, in particular those for the calcaneum, are quite different from those present in the other forms. Both *Amphicyon* and *Felis* have these two facets joined by a narrow connection, a condition not present in *Ursus* or *Canis*. The second facet in *Felis* (Fig. 18, F-1) has an additional articular surface projecting in a plantar direction from the medial edge of this surface. The facet for the distal end of the fibula is well developed in *Amphicyon*, in keeping with the size of that unusually heavy bone. The surface for articulation with the navicular is proportionately of nearly the same size in *Amphicyon* and *Ursus* and is relatively larger than in *Felis* or *Canis.*

The calcaneum (Fig. 19) is known from eight specimens. In *Felis* the area of the sustentacular facets is notable for being more compressed laterally than in the other forms. *Amphicyon* and *Ursus* are nearly alike in the proportions of this part of the calcaneum, and *Canis* is intermediate between these and *Felis.* Present in the puma, but not in the others, is a groove for the tendon of the peroneus longus muscle, which extends the foot upon the leg and everts the sole of the foot. This groove is situated at the medial border of the articular notch at its junction with the cuboid surface (Fig. 20, F-2). This strong development in the cat, alone among the forms examined, may be correlated with the more vigorous springing action characteristic of this animal.

A well defined groove or sulcus is present in *Amphicyon* along the base of the sustentaculum at its junction with the tuber calcis. This groove is of nearly the same proportions in *Amphicyon* and *Ursus*, much deeper and narrower in *Felis,* and barely evident in *Canis.* The proximal face of the dorsal surface of the calcaneum, between the facet for the cuboid and the facets for the astragalus, exhibits in *Amphicyon* a well defined scar for M. extensor digitorum brevis. .This muscle acts to extend the toes, and its scar is much more evident in the puma and *Amphicyon* than in the other two. The distal end of the tuber calcis in both *Amphicyon* and *Felis* has a well defined groove for the insertion of the tendon of Achilles. This groove is less evident in *Ursus* and *Canis.* The scars, on the posterior face of the proximal end of the calcaneum, for the attachment of the plantar ligaments are equally well developed in all. The width of the sustentaculum is proportionately equal in *Amphicyon* and *Ursus*, considerably narrower in *Felis* and *Canis.* The sustentacular area is particularly prominent in those mammals that walk more or less on the soles of their feet, such as man and bear. The resemblance here between *Amphicyon* and *Ursus* may indicate that both forms had about the same degree of plantigradism.

The only known navicular of *Amphicyon* (Fig. 20, A-1 to A-6) is unfortunately somewhat broken, so that it is impossible to be certain as to whether or not a proximal tuberosity, such as occurs in felids and in some canids (Fig. 20, F-6 and C-6), but not in *Ursus*, was present. The general shape of the articulation with the ectocuneiform and mesocuneiform, is nearly the same in *Amphicyon* and *Ursus.* This bone in *Felis* differs from the others in having a noticeably deeper groove running from the tuberosity along the plantar margins of the articular facets.

The ectocuneiform is distinctive in each form. In *Amphicyon* (Fig. 20, A-11) the plantar projection is more hooklike. This projection is well developed but less hooked in *Canis,* and is much reduced in *Ursus.* In *Felis* this projection terminates in a mushroom-like tip. The articular surface for metatarsal III is triangular in shape in *Amphicyon*, *Ursus* and *Canis*, "hourglass-shaped" in *Felis.* The facet for the navicular is nearly square in *Amphicyon* and *Ursus,* and convex in the former, while it is triangular and concave-shaped in *Felis* and *Canis.* The facets for metatarsals and cuboid are much larger proportionately in *Amphicyon* than in the other forms.

The cuboid of *Amphicyon* (Fig. 20, A-13 to A-18) is distinctive in that all of the facets are relatively large. The groove and projection for the tendon of the peroneus longus muscle are very well developed; the former is deeper than in *Ursus* or *Canis* but of about the same depth as in *Felis.*

The elements of digit III (Fig. 21) only will be discussed in any detail. The other digits of *Amphicyon* show essentially similar resemblances to and differences from those of the other forms.

Metatarsal III of *Amphicyon* is quite like that of the bear, differing only in being rather heavier at the proximal end. That of *Felis* is proportionately much longer and more slender, and is seen to be slightly curved when viewed from the side. The facets for the adjoining metatarsals are essentially similar in *Amphicyon*, *Ursus* and *Felis*, those of *Canis* being smaller. The facet for the ectocuneiform is hammer-shaped in *Amphicyon* and *Ursus*, with a smaller median constriction than occurs in *Felis.* In *Canis* the anterior portion of this facet differs strikingly from those of the other forms in lacking a projecting wing at the angle nearest to metatarsal II.

The proximal phalanges of digit III of *Amphicyon*, the bear and puma are nearly the same as regards proportions; that of the dog is straighter and narrower.

The median phalanges have nearly the same form in *Amphicyon* and *Ursus*, those of *Canis* being proportionately more slender. *Felis* differs from all others in having a recess for the ungual phalanx and a tendinal scar (Fig. 21, F-6), as described above under the forefoot.

CONCLUSIONS

In a carnivore of this type the carnassial teeth have lost much of their shearing function and the molar teeth are more square in outline, having blunt cusps with the lower surface of the crowns complicated by a wrinkling of the enamel. These features of the dentition plus the retention of M^3 are suggestive of a departure from the predominantly meat-eating habits of the dogs and intimate instead an omnivorous diet similar to that of the true bears.

Although the skull and lower jaws are canid-like in form, the otic region is unlike anything known in canids and instead more nearly resembles that of the ursids. *Hemicyon*, which I regard as a bear, is similar to *Amphicyon* in skull form but its dentition and otic region are even more like the true ursids than are those of *Amphicyon*.

The postcranial skeleton of *Amphicyon* is proportionately heavier than in any member of the Canidae and the limbs and feet are close to those of the true ursids. I find nothing in the morphological features of the skeleton of *Amphicyon* to link this form with the felids.

Drawing the canid-ursid line, on the evidence of the dentition and skeleton, the Ursidae become distinct above the Oligocene with *Daphoenodon* and *Amphicyon* forming an offshoot from this main ursid line during the Miocene and becoming extinct before the middle Pliocene. I believe that the affinities of *Amphicyon* and *Daphoenodon* are with the bears and propose that the subfamily Amphicyoninae, usually included under the Canidae, be transferred to the Ursidae.

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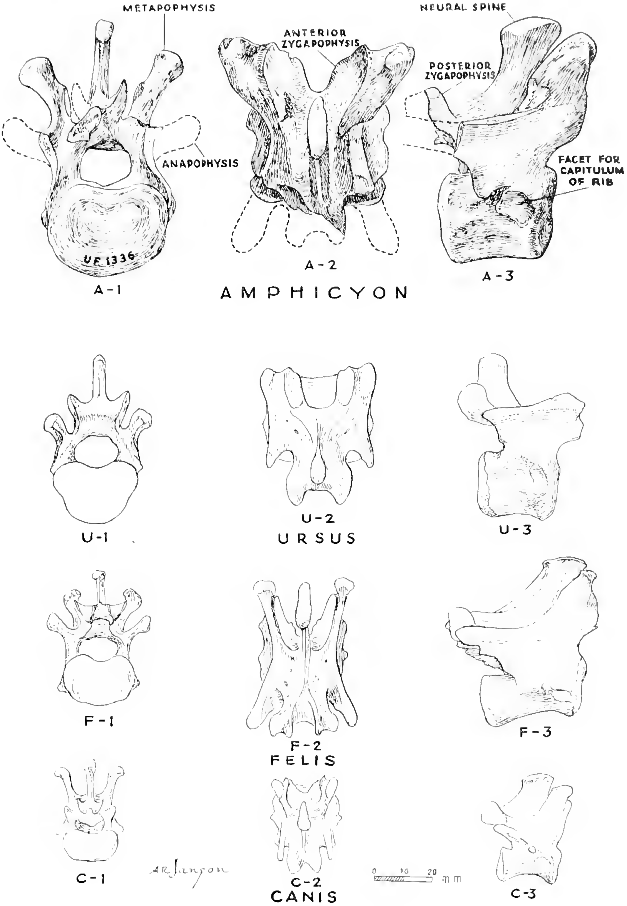


Figure 1

Thirteenth thoracic vertebra

Amphicyon. A-1, posterior view; A-2, dorsal view; A-3, lateral view. Comparable views for *Ursus, Felis* and *Canis.*

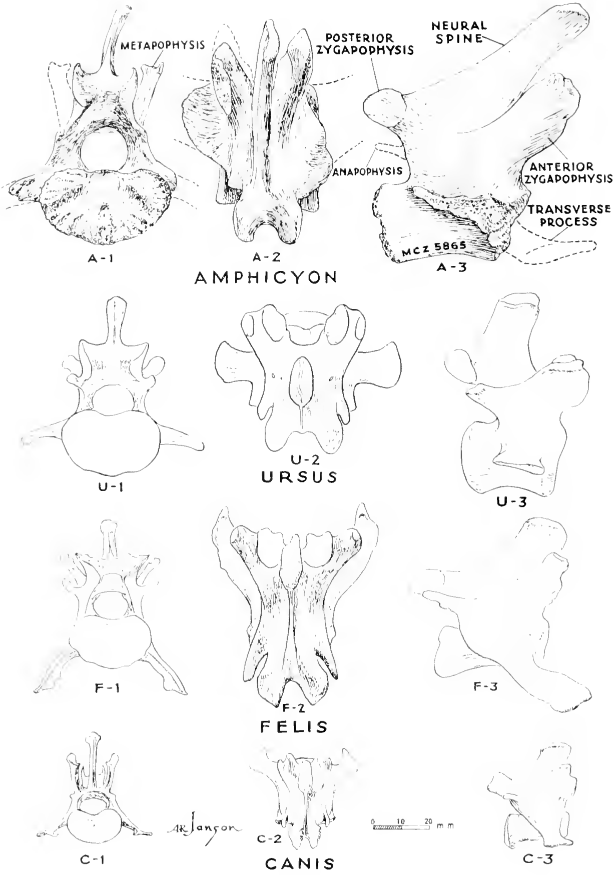


Figure 2

Second lumbar vertebra

Amphicyon. A-1, posterior view; A-2, dorsal view; A-3, lateral view. Comparable views for *Ursus*, *Felis* and *Canis*.

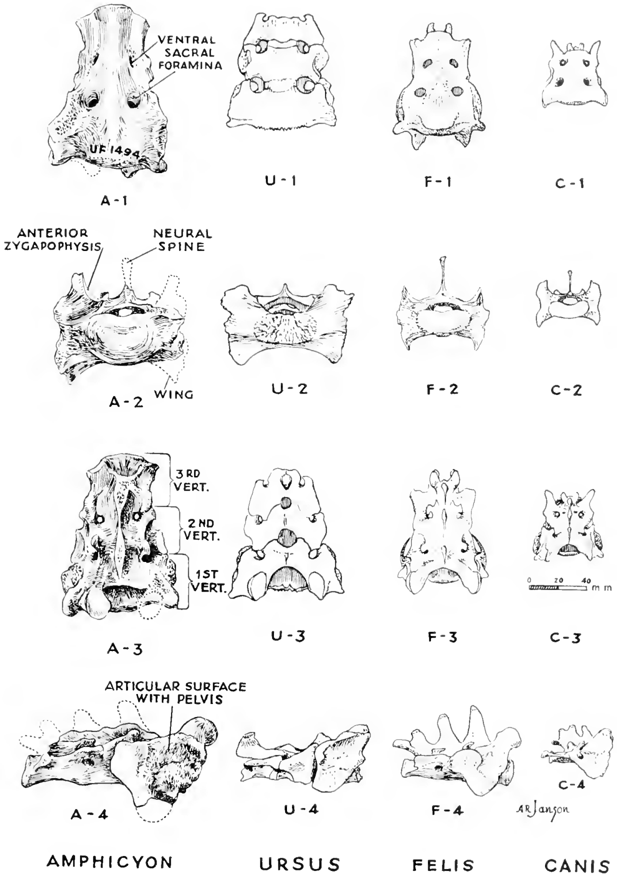


Figure 3

Sacrum

Amphicyon. A-1, ventral view; A-2, anterior view; A-3, dorsal view; A-4, lateral view. Comparable views for *Ursus*, *Felis* and *Canis*.

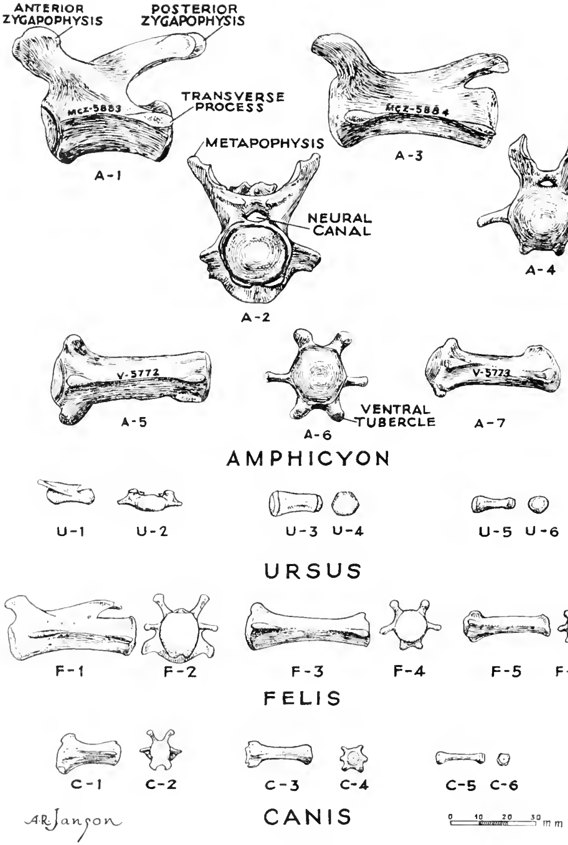


Figure 4
Caudal vertebrae

Amphicyon. A-1, lateral view seventh caudal; A-2, anterior view, seventh caudal; A-3, lateral view, ninth caudal; A-4, anterior view, ninth caudal; A-5, lateral view, twelfth caudal; A-6, anterior view, twelfth caudal; A-7, lateral view, seventeenth caudal. *Ursus:* U-1, U-2, lateral and anterior views, third caudal; U-3, U-4, lateral and anterior views, seventh caudal; U-5, U-6, lateral and anterior views, ninth caudal. *Felis:* F-1, F-2, lateral and anterior views, seventh caudal; F-3, F-4, lateral and anterior views, twelfth caudal; F-5, F-6, lateral and anterior views, seventeenth caudal. *Canis:* C-1, C-2, lateral and anterior views, seventh caudal; C-3, C-4, lateral and anterior views, twelfth caudal; C-5, C-6, lateral and anterior views

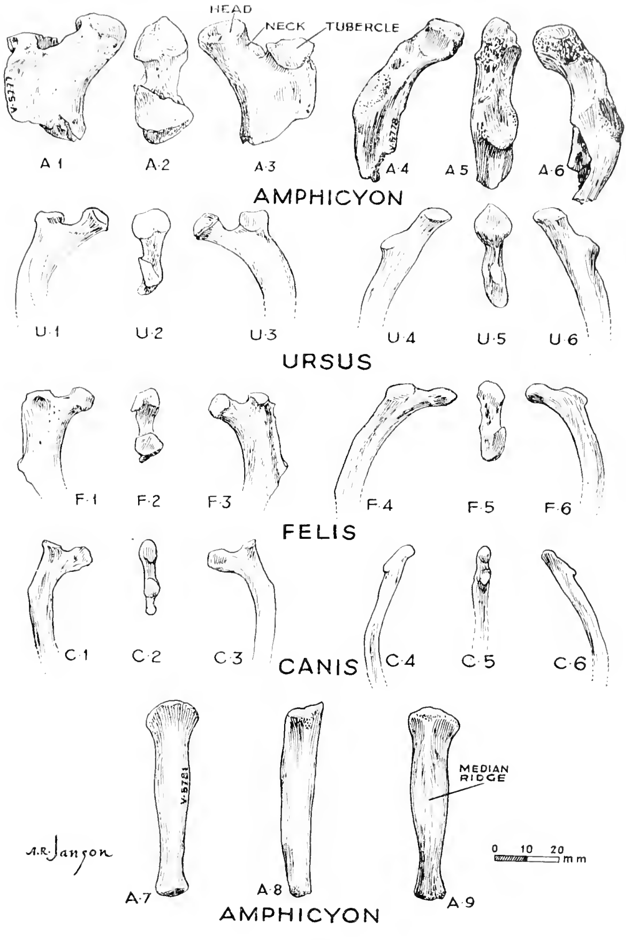


Figure 5
Ribs and Xiphisternum

Amphicyon. A-1, anterior view, third right rib head; A-2, articular view of third right rib head; A-3, posterior view of third right rib head; A-4, posterior view of eleventh left rib head; A-5, articular view of eleventh left rib head; A-6, anterior view of eleventh left rib head. Comparable views

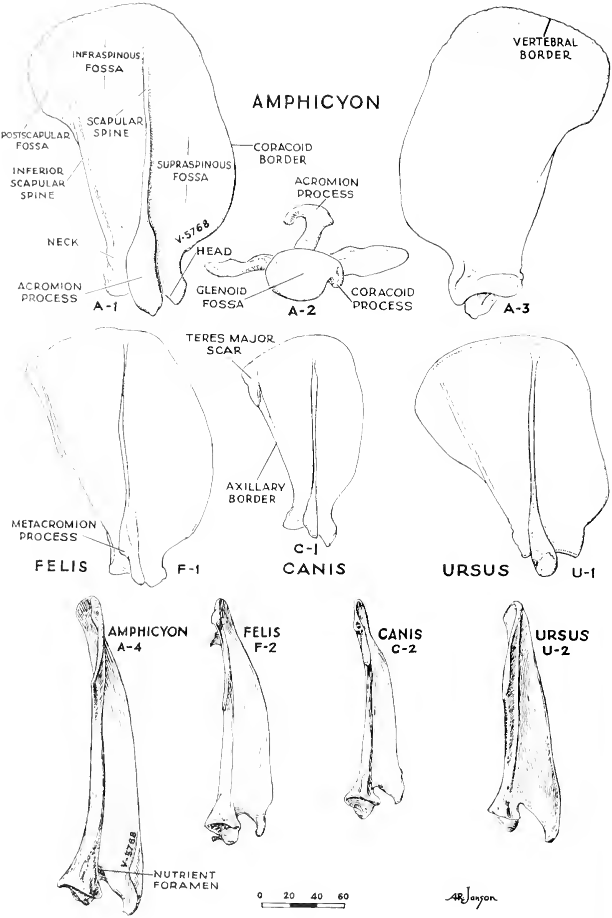


Figure 6
Right scapula

Amphicyon. A-1, lateral view; A-2, glenoid view; A-3, medial view; A-4, view from axillary border. Comparable views for *Ursus, Felis* and *Canis.*

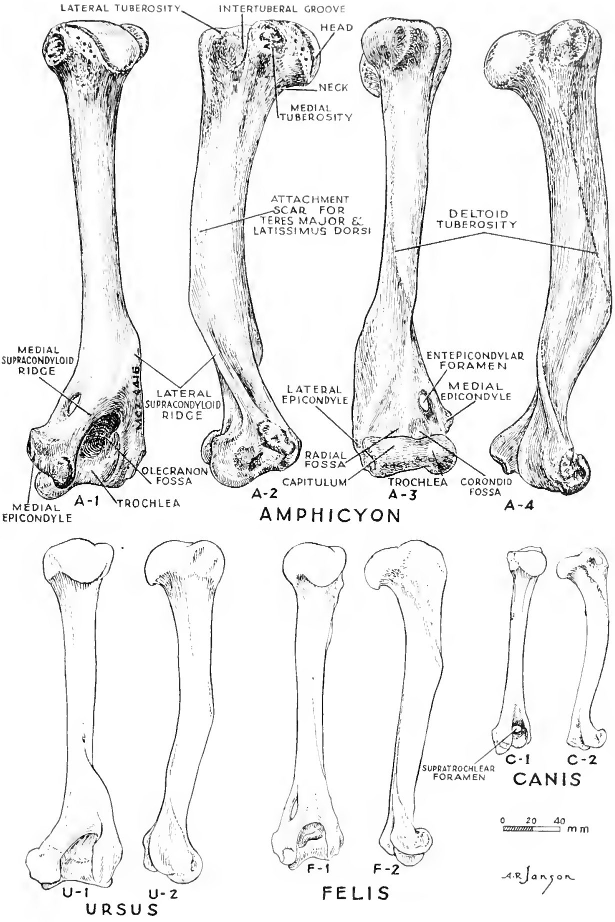


Figure 7
Right humerus

Amphicyon. A-1, anterior view; A-2, medial view; A-3, posterior view; A-4, lateral view. Comparable views for *Ursus*, *Felis* and *Canis*.

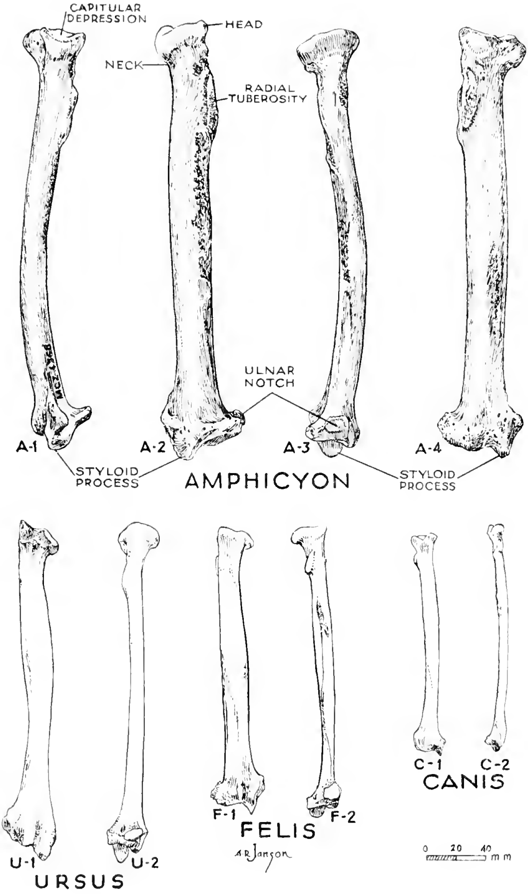


Figure 8
Right radius

Amphicyon. A-1, anterior view; A-2, medial view; A-3, posterior view; A-4, lateral view. Comparable views for *Ursus*, *Felis*, and *Canis*.

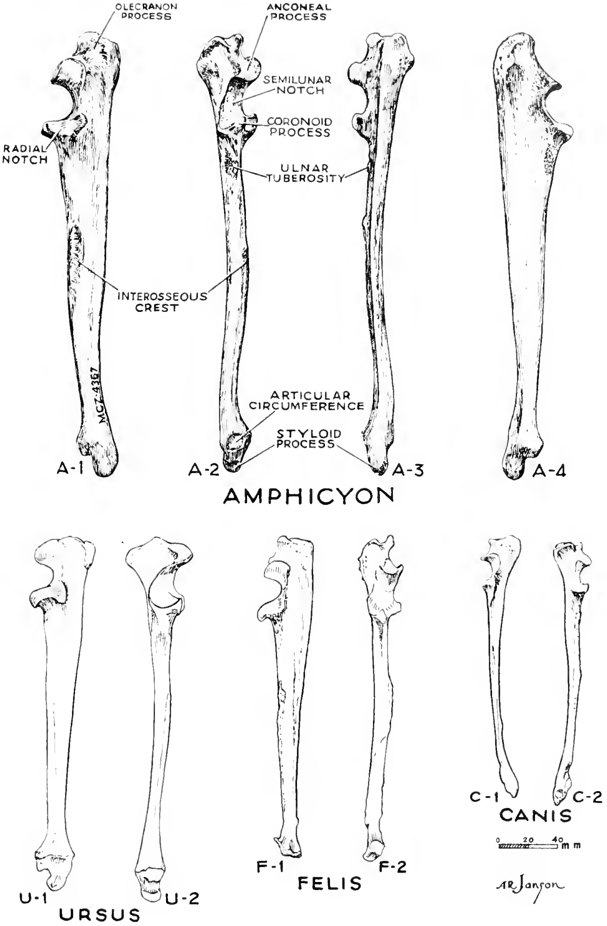


Figure 9
Left ulna

Amphicyon. A-1, lateral view; A-2, anterior view; A-3, posterior view; A-4, medial view. Comparable views for *Ursus, Felis* and *Canis.*

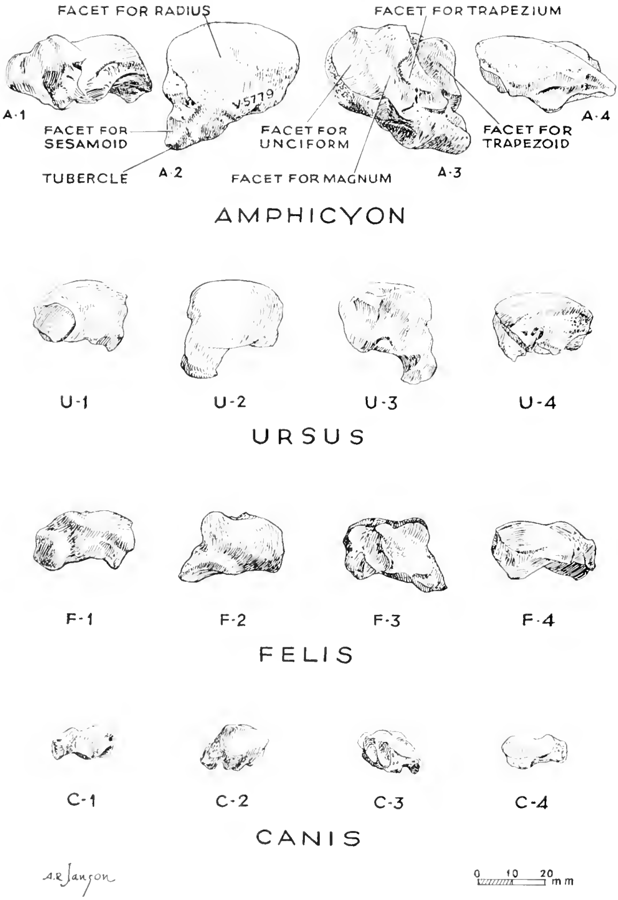


Figure 10
Right scapho-lunar

Amphicyon. A-1, medial view; A-2, proximal view; A-3, distal view; A-4, dorsal view. Comparable views for *Ursus, Felis* and *Canis.*

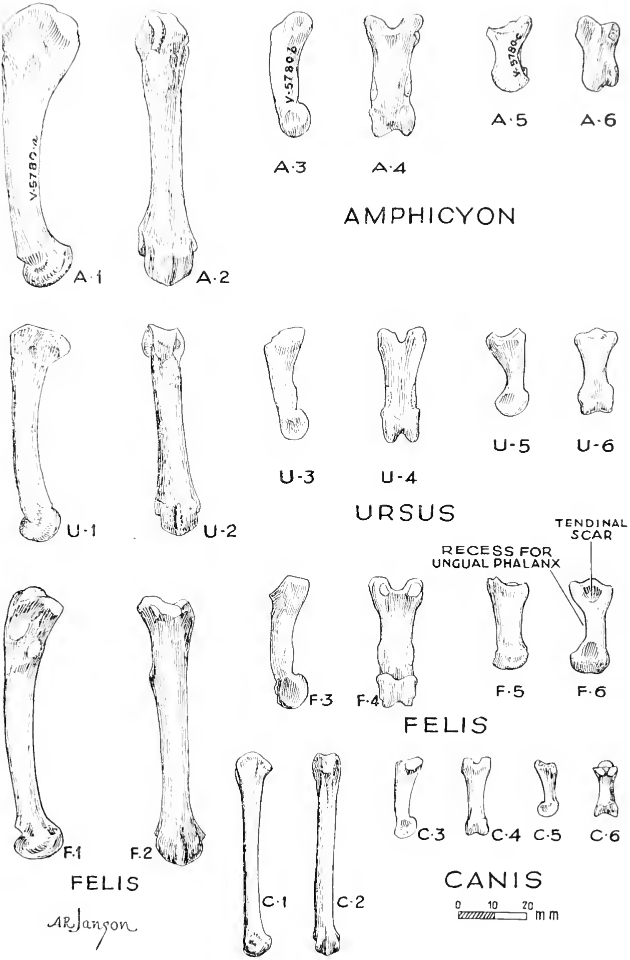


Figure 11

Left metacarpal III, proximal and middle phalanges

Amphicyon. A-1, A-2, lateral and volar views, metacarpal III; A-3, A-4, lateral and volar views, proximal phalanx; A-5, A-6, lateral and volar views, middle phalanx. Comparable views of *Ursus*, *Felis* and *Canis*.

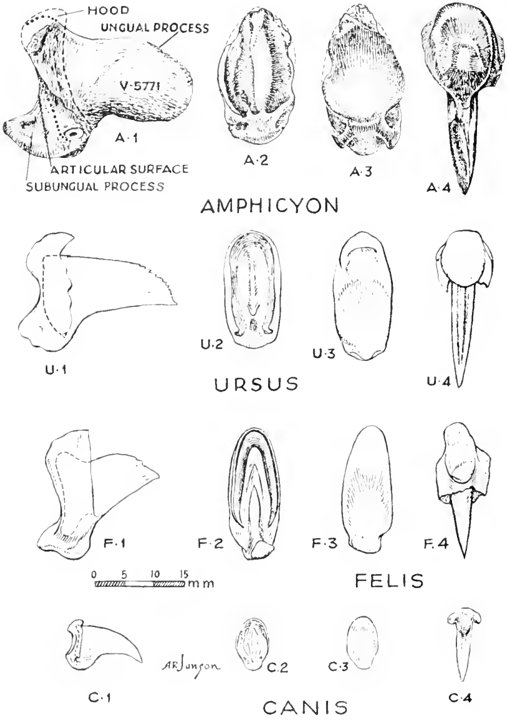


Figure 12
Distal phalanx

Amphicyon. A-1, lateral view; A-2, anterior view; A-3, posterior view; A-4, volar view. Comparable views for *Ursus*, *Felis* and *Canis*.

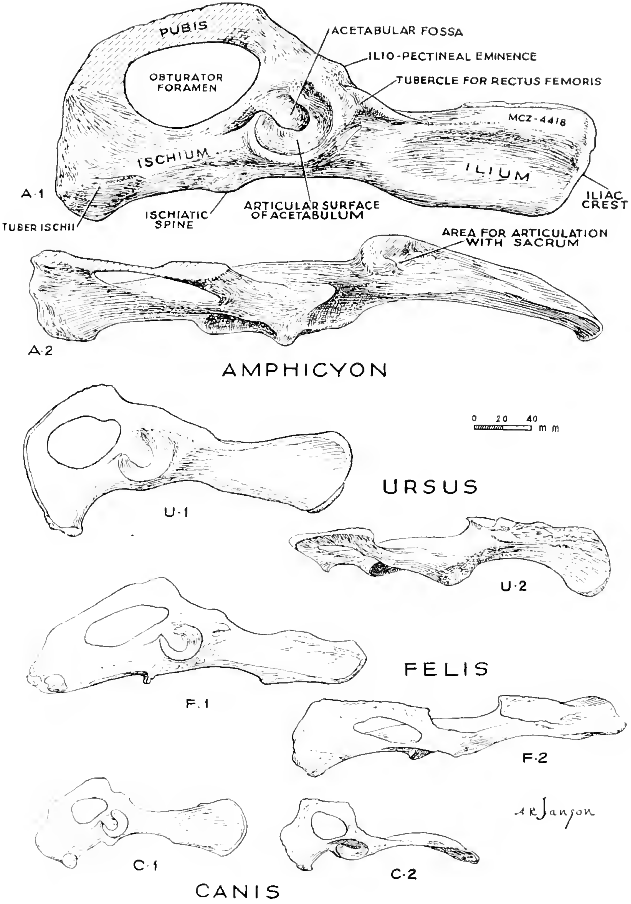


Figure 13
Left innominate

Amphicyon. A-1, lateral view; A-2, ventral view. Comparable views for *Ursus, Felis* and *Canis.*

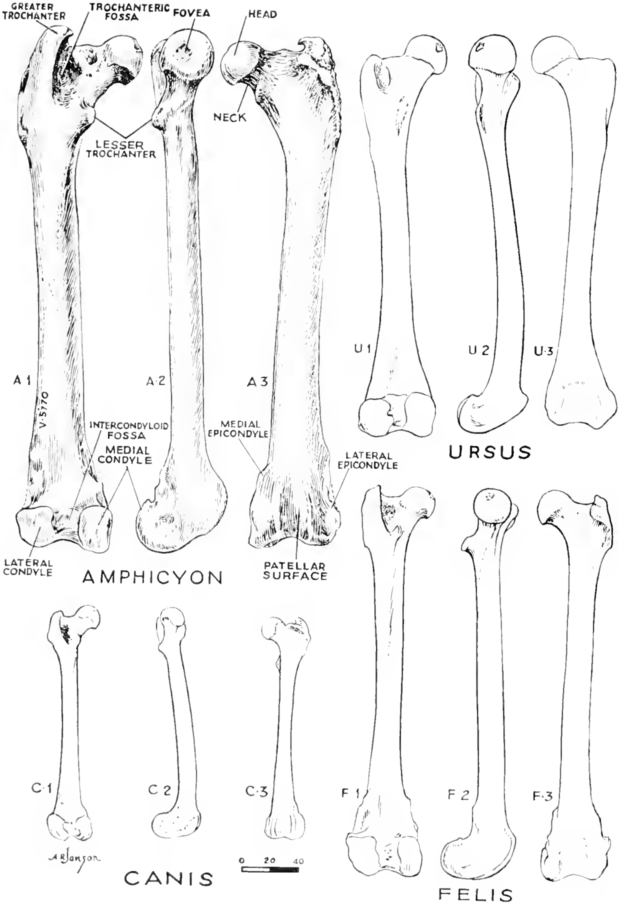


Figure 14
Left femur

Amphicyon. A-1, posterior view; A-2, medial view; A-3, anterior view. Comparable views for *Ursus, Felis* and *Canis.*

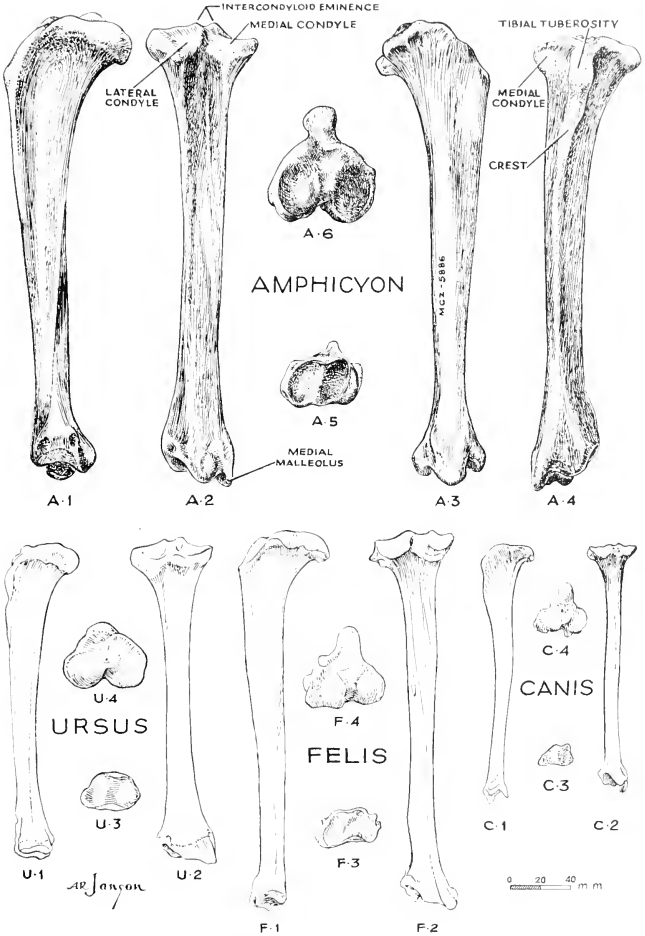


Figure 15
Left tibia

Amphicyon. A-1, lateral view; A-2, posterior view; A-3, medial view; A-4, anterior view; A-5, distal view; A-6, proximal view. Comparable views of *Ursus, Felis* and *Canis.*

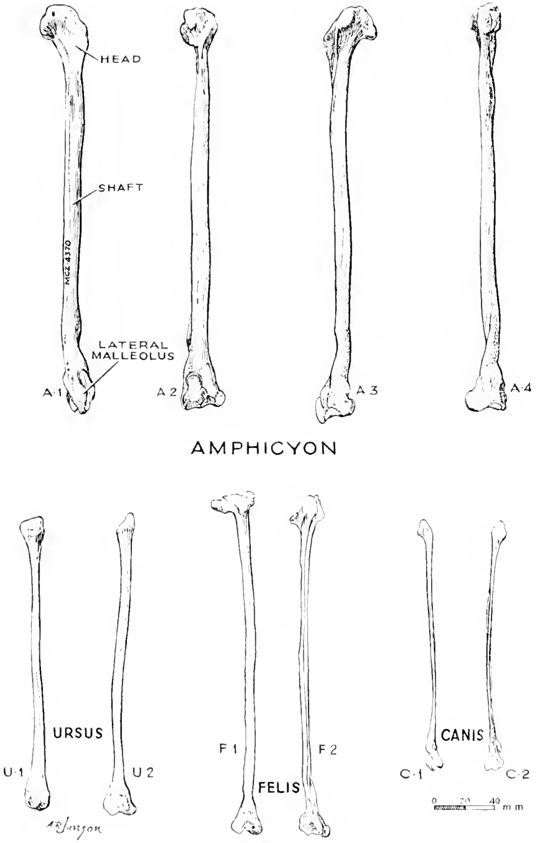


Figure 16
Right fibula

Amphicyon. A-1, anterior view; A-2, medial view; A-3, posterior view; A-4, lateral view. Comparable views for *Ursus*, *Felis* and *Canis*.

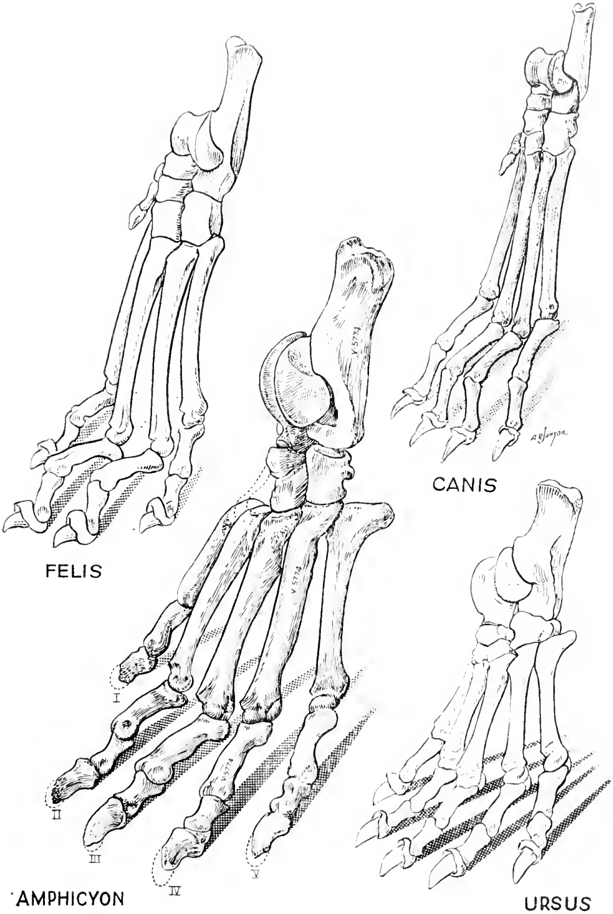


Figure 17

Articulated left hind feet of *Amphicyon*, *Ursus*, *Felis* and *Canis*. All shown in same phase of stride.

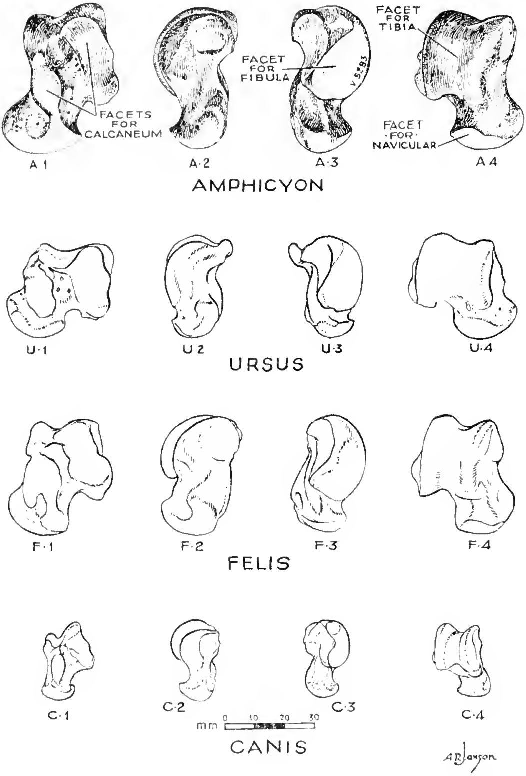


Figure 18
Right astragalus

Amphicyon. A-1, volar view; A-2, medial view; A-3, lateral view; A-4, dorsal view. Comparable views for *Ursus, Felis* and *Canis.*

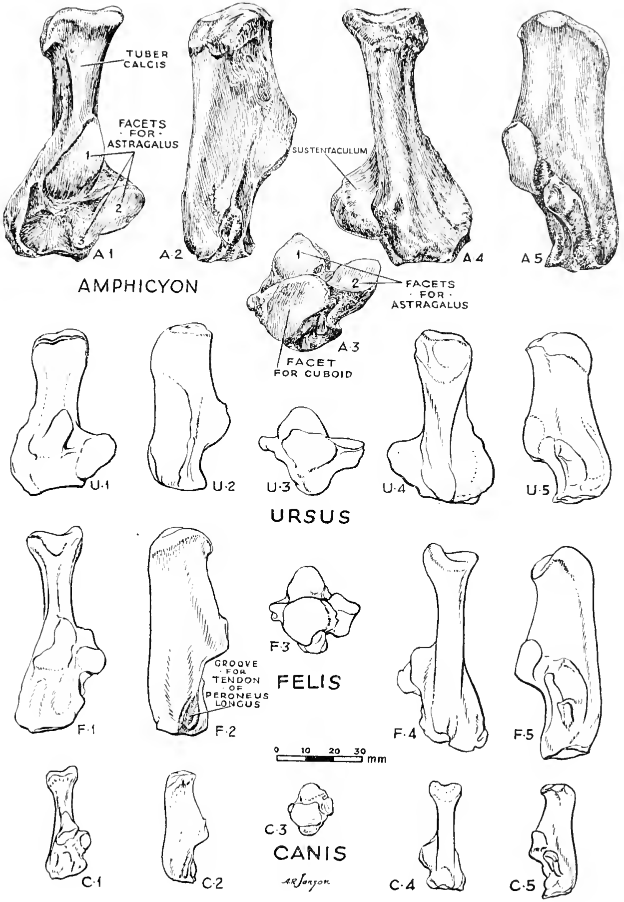


Figure 19
Right calcaneum

Amphicyon. A-1, dorsal view; A-2, lateral view; A-3, volar view; A-4, posterior view; A-5, medial view. Comparable views for *Ursus, Felis* and *Canis.*

Figure 20

Left navicular, ectocuneiform and cuboid

Amphicyon navicular. A-1, dorsal view; A-2, lateral view; A-3, volar view; A-4, medial view; A-5, proximal view; A-6, distal view.

Ursus navicular. U-1 to U-6, same views as *Amphicyon.*

Felis navicular. F-1 to F-6, same views as *Amphicyon.*

Canis navicular. C-1 to C-6, same views as *Amphicyon.*

Amphicyon ectocuneiform. A-7 to A-12, same views as *Amphicyon* navicular.

Ursus ectocuneiform. U-7 to U-12, same views as *Amphicyon.*

Felis ectocuneiform. F-7 to F-12, same views as *Amphicyon.*

Canis ectocuneiform. C-7 to C-12, same views as *Amphicyon.*

Amphicyon cuboid. A-13 to A-18, same views as *Amphicyon* navicular.

Ursus cuboid. U-13 to U-18, same views as *Amphicyon.*

Felis cuboid. F-13 to F-18, same views as *Amphicyon.*

Canis cuboid. C-13 to C-18, same views as *Amphicyon.*

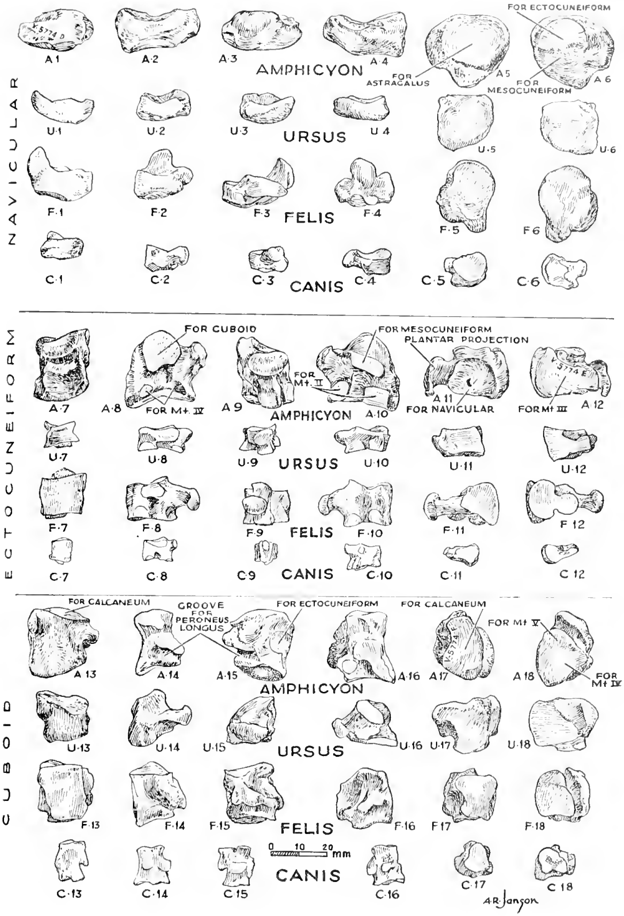


Figure 20
Left navicular, ectocuneiform and cuboid

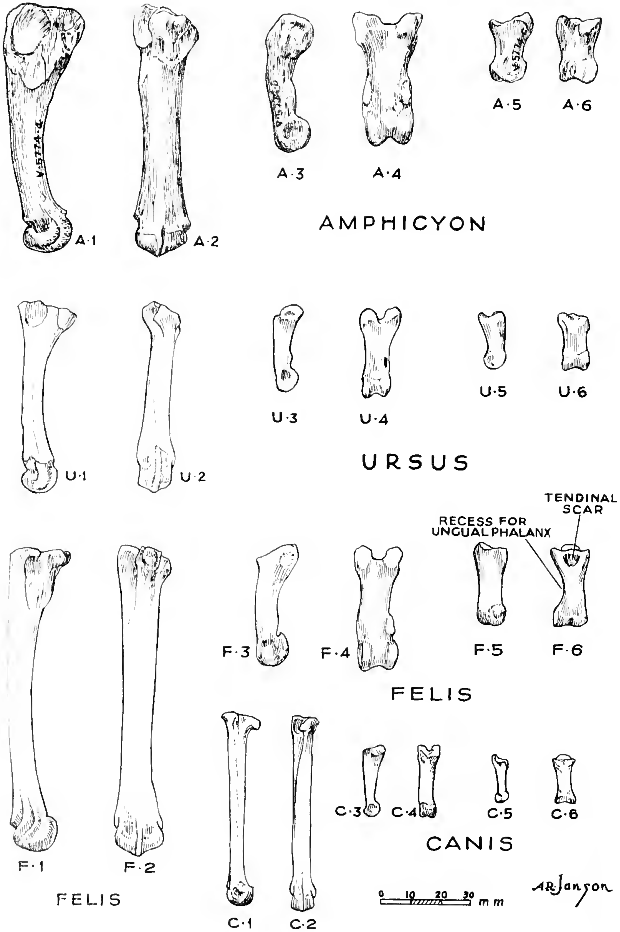
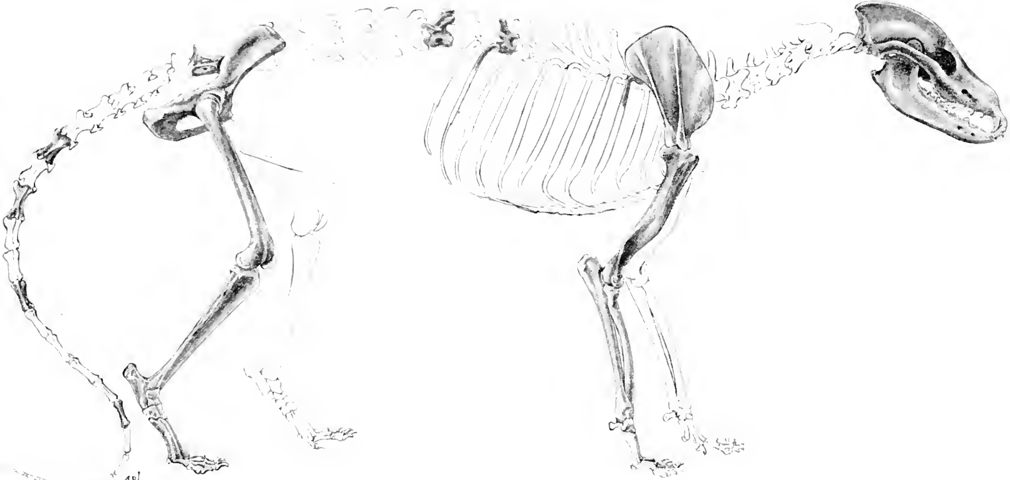


Figure 21
Left metatarsal III, proximal and middle phalanges

Amphicyon. A-1, A-2, lateral and volar views of metatarsal III; A-3, A-4, lateral and volar views of proximal phalanx; A-5, A-6, lateral and volar views of middle phalanx. Comparable view for *Ursus, Felis* and *Canis.*



Amphicyon longiramus

COMPOSITE RESTORATION · KNOWN ELEMENTS ARE INDICATED BY DETAILED SHADING

PLATE

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 123, No. 2

A REVIEW OF THE PARDALIS-MACULATUS COMPLEX OF THE BOID GENUS TROPIDOPHIS OF THE WEST INDIES

By Albert Schwartz and Robert J. Marsh

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
September, 1960

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No. 2 *A review of the* PARDALIS-MACULATUS *complex of the boid genus* TROPIDOPHIS *of the West Indies.*

BY ALBERT SCHWARTZ AND ROBERT J. MARSH[1]

The small, multispotted boas of the genus *Tropidophis*, in the West Indies, have proven a troublesome group to many American workers concerned with West Indian herpetology. This is especially true if one is interested in Cuban reptiles, since the complex is represented there by several forms. On Cuba, as well, occur representatives of two other major groups of the genus, the larger, and keeled-scaled *T. melanurus* and the prominently and contrastingly spotted group consisting of *T. semicinctus*, *T. wrighti* and *T. feicki* (Schwartz, 1957). In the present paper we will attempt to clarify the relationships in the nominal species *T. pardalis* and *T. maculatus*, as well as those of *T. nigriventris*. The situation appears to be far more complicated than has been previously considered, and it has only been through the assembling of much material that the present conclusions have been reached.

The only attempt to revise the genus *Tropidophis* is that of Stull (1928). At the time of this revision, there were 177 specimens of the genus in collections in the United States; these specimens represented eleven of the thirteen forms which Miss Stull regarded as valid. These thirteen forms were divided by her into two major groups: 1) the *maculatus* group (including the named forms *maculatus*, *jamaicensis*, *haetianus*, and *paucisquamis*) characterized by smooth scales, bifurcate and longitudinally laminate hemipenes; and 2) the *pardalis* group (*taczanowskyi pardalis*, *canus*, *curtus*, *androsi*, *bucculentus*, *wrighti*, *melanurus*, and *semicinctus*) characterized by more or less keeled scales, and a quadrifurcate hemipenis which is longtudinally flounced in the secondary forks and transversely flounced in the primary forks. Of these named forms, we have concerned ourselves with the South American *taczanowskyi* and *paucisquamis* only briefly and not at all with the distinct *melanurus* (and its Cayman subspecies *parkeri* and *caymanensis*; see Grant, 1941a), nor the *semicinctus* complex as noted above. The snake regarded as *T. pardalis bucculentus* by Miss Stull is considered by us as more closely related to *T. melanurus*, as Bailey (1937 :45) has pointed out, and thus not within the province of the present paper.

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Since the publication of Miss Stull's revision, several other snakes belonging to the complex under study have been described. In 1936, Barbour and Shreve described *T. pardalis greenwayi* on the basis of two specimens from Ambergris Cay, Caicos Islands, in the Bahamas. Bailey (*op. cit.*) later described *T. nigriventris* and *T. maculatus pilsbryi* from limited material from Cuba and *T. pardalis barbouri* from several islands in the Bahamas; finally, in 1940, Grant described two new forms from Jamaica, *T. pardalis stejnegeri* and *T. maculatus stulli*. The named forms which we will consider in this paper thus include the following:

Tropidophis pardalis pardalis Gundlach, 1840
Tropidophis pardalis canus Cope, 1868
Tropidophis pardalis curtus Garman, 1887
Tropidophis pardalis androsi Stull, 1928
Tropidophis pardalis greenwayi Barbour and Shreve, 1936
Tropidophis pardalis barbouri Bailey, 1937
Tropidophis pardalis stejnegeri Grant, 1940
Tropidophis maculatus maculatus Bibron, 1840
Tropidophis maculatus haetianus Cope, 1879
Tropidophis maculatus jamaicensis Stull, 1928
Tropidophis maculatus pilsbryi Bailey, 1937
Tropidophis maculatus stulli Grant, 1940
Tropidophis nigriventris Bailey, 1937

We have examined 229 snakes representing the above forms; we wish to thank the following curators for their most generous loans of material, without which we would have been unable to undertake the present task: Mr. Charles M. Bogert, American Museum of Natural History (AMNH); Dr. James Boehlke and Mr. Edmund V. Malnate, Academy of Natural Sciences of Philadelphia (ANSP); Sr. Miguel L. Jaume García, Museo y Biblioteca de Zoología de la Habana (MBZH); Dr. Ernest E. Williams, Museum of Comparative Zoology (MCZ); Dr. Carlos G. Aguayo y de Castro and Dr. Isabel Pérez Farfante, Museo Poey (MP); Dr. Norman E. Hartweg, Museum of Zoology, University of Michigan (UMMZ); Mr. Oscar T. Owre and Mr. Dennis R. Paulson, University of Miami (UMRC); and Dr. Doris M. Cochran, United States National Museum (USNM). The collections from the Museo Poey and the Museo y Biblioteca de Zoología de la Habana are extremely interesting, pertinent, and valuable, and have heretofore not been available to American workers; we are especially grateful to Drs. Aguayo and Farfante.

and to Sr. Jaume for the privilege of examining the snakes under their care. The illustrations are the work of Mr. Ronald F. Klinikowski, whose work was supported by a National Science Foundation grant, and we wish to express our sincere appreciation to him for his time and efforts on our behalf.

Throughout the remainder of the text, the use of a trivial name only refers to specimens regarded as assigned to that named population and does not imply that relationships are quite as indicated in the list of recognized forms above. We have examined the following numbers of specimens from the West Indies: *androsi*, 10; *barbouri*, 15; *canus*, 20; *curtus*, 30; *greenwayi*, 2; *haetianus*, 11; *jamaicensis*, 11; *maculatus*, 17; *nigriventris*, 5; *pardalis*, 75; *pilsbryi*, 4; *stejnegeri*, 4; *stulli*, 2. In addition, there are four specimens from Cuba, one from the Cay Sal Bank, and 17 from the Bimini Islands, all of which require special comment. Insofar as we are concerned, all these named populations are valid, and no names will be regarded as synonyms; however, the degree of distinctness of the various forms varies greatly, and this criterion has been used to differentiate both subspecies and species in the present paper.

The following data have been taken on each specimen, as far as practicable; a few individual snakes have been so long in preservative that the details of pattern are faded and poorly shown, and a few others were probably preserved in strong alcohols and consequently are now almost worthless for study, but the majority of snakes have been completely useful. Pertinent data on all populations are given in Table I.

1) sex — since all males of this complex possess a pair of small spurs at the vent, distinguishing them from females is comparatively easy. Occasionally these spurs are small and partially retracted; in all dubious specimens dissection of the hemipenes was made.
2) total length, in millimeters
3) length of tail, in millimeters
4) number of ventral scales — counted in the manner proposed by Dowling (1951)
5) number of unpaired subcaudal scales, including terminal spine
6) number of supra- and infralabials
7) number of pre- and postoculars
8) number of scale rows around body behind head, at midbody, and anterior to vent

9) presence or absence of contact between the parietal plates
10) number of longitudinal rows of body blotches, counted around body at midbody; this includes blotches on the venter
11) presence or absence of a pair of light occipital spots, easily distinguished from the dark dorsal ground color
12) color of the tip of the tail — either dark (including any coloration from tawny to olive to black) or light (undifferentiated from the remainder of the pale dorsal ground color or distinctly lighter than the dorsal ground color, probably yellow in life).
13) number of blotches, on right and left sides, in the two paramedian dorsal rows of blotches, counted from the first dark blotches behind the head to those just anterior to the vent
14) number of blotches on the dorsum of the tail; this count is subject to extreme variation since the caudal blotches may be paired, either regularly or irregularly, fused into dorsal saddles, alternating, or extremely reduced in extent.
15) keeling of dorsal scales — checked on dorsal rows of scales, especially above vent

Stull's grouping

Miss Stull (*op. cit.*:3-4) divided the forms of *Tropidophis* into two major groups, as noted above. The basis for this division was the character of the dorsal scales and the type of hemipenis, either bi- or quadrifurcate. The members of the *pardalis* group were represented as having the dorsal scales always more or less keeled ("varying from strong keeling even in young specimens . . . to weak keeling only in the most dorsal rows of full grown adults": Stull, *loc. cit.*), whereas the *maculatus* group was considered as having smooth scales. This difference appears not to exist when large series of specimens are considered. First, of 62 specimens of *pardalis* examined, 60 have the dorsal scales completely *smooth*, and only two have any indication of dorsal keeling; this is in definite contrast to Stull's statement as quoted above. Secondly, of 19 *maculatus*, eleven have distinct dorsal keels, and eight have these scales smooth; thus the basic character of smooth versus keeled scales as a primary character in distinguishing the "*pardalis*" from the "*maculatus*" group is useless, since the taxa from which the group names have been taken are variable in this particular character, and Stull's original diagnoses of the groups is based upon inadequate data and material. That the situation reported here for the forms *pardalis* and *maculatus* is not unusual is shown by the fact that, if more than only a very few specimens of a taxon are available, both smooth and keeled dorsals are demonstrable in the material. In *jamaicensis* all specimens (ten) on which carination was determinable had smooth dorsals; this is the largest number of specimens representing a single taxon in which only one type of dorsal (keeled or smooth) occurs with consistency throughout the sample. Occasionally, even in small samples both types of scales are demonstrated; of four *pilsbryi*, three have the dorsals keeled and one has them smooth.

The carination of dorsals thus appears to be an invalid criterion in these boids; however, there are *tendencies* within populations toward either a preponderance of keeled or smooth dorsals. Thus the vast majority of *pardalis* have smooth scales (97%), most *curtus* have keeled scales (90%), most *haetianus* have smooth scales (91%), etc. The carination apparently does not depend upon either sex or ontogenetic changes; both males and females, and adults and young, appear to be indiscriminately keeled or smooth, without any obvious correlation. The two keeled *pardalis*, for example, are a juvenile female and an adult male, from two widely separated localities. To ascertain whether the dorsals are keeled or smooth is sometimes extremely difficult. In many instances the preservation and subsequent drying may have wrinkled the scales or curled them around the edges; some snakes have the dorsals much pitted or eroded (this is especially true of Bahaman snakes). All such dubious cases were left unrecorded, and it is probable that proportions in certain instances would be somewhat changed had we been able to determine this character on all specimens. Nonetheless, we feel certain that carination *per se* is not an all-or-none phenomenon in the *pardalis-maculatus* complex, and must be used with caution in diagnosing groups, with emphasis rather on tendencies within populations.

Stull's second character, that of the forking of the hemipenis, is apparently equally untenable. We have examined by dissection the hemipenes of all forms pertinent to the study. In addition, a few recently preserved specimens have the hemipenes extruded. In no cases have we seen quadrifurcate hemipenes. The appearance of double bifurcation is at times given by the bands of retractor muscle fibers, but in every case where this superficial resemblance to a quadrifurcate hemipenis was seen upon dissection, careful observation revealed that the hemipenis was in actuality bifurcate. Extruded hemipenes (*nigriventris, barbouri, jamaicensis, pardalis*) likewise are uniformly bifurcate and show no evidence of the quadrifurcate condition. It is pertinent to point out here that Stull (*op. cit.*:11) cited only a single male (MCZ 12445) of *maculatus* examined; we have studied this snake. It lacks spurs, and the tail has been dissected; what were apparently considered as being hemipenes are in reality the paired scent glands, filled at present with much fragmented and solidified musk. The snake is obviously a female; however, dissection of available *maculatus* males reveals that they do indeed have a bifurcate hemipenis, as do all other known members of the complex.

In summary, we are unable to differentiate between the "*pardalis*" and "*maculatus*" groups on the basis of the structure of the hemipenes; all have a bifurcate rather than a quadrifurcate structure. Stull's original statements concerning the two types of hemipenes in the snakes involved have almost certainly led other workers (Bailey, *op. cit.*:49) to attempt to relate more recently described forms to one or the other group with possible subsequent confusion. Both the characters used by Stull to differentiate these two basic groups have been shown to be invalid, at least insofar as the *pardalis-maculatus* complex is concerned. We do not know what type of hemipenes occur in the South American forms (*T. paucisquamis* appears to have a bifurcate hemipenis), in *melanurus*, and in the *semicinctus* aggregate.

Size

We have no assurance, of course, that we have seen maximally sized individuals of both sexes in all cases. This is especially true of taxa which are represented by small series, and in two cases (*stulli, greenwayi*) we have studied members of only one sex, and in another (*pilsbryi*) have not seen adult females. Consequently, comments on size are open to obvious criticism; however, general trends can be noted and statements appropriately made.

The largest size among males is reached by *stejnegeri* (416 mm. in total length); the largest size among females is reached by *haetianus* (712 mm.). In six forms (*pardalis, stejnegeri, jamaicensis, canus, curtus, barbouri*), males reach a larger size than females; of these, *stejnegeri* is represented by three females and one male. In two forms (*maculatus, haetianus*), females reach a larger size than males. In two forms (*androsi, nigriventris*), both sexes reach an equal size.

By ranking the largest individual of each sex of each form, a tentative index of overall size relative to the other members of the complex can be reached; since inadequate data are at hand for *pilsbryi, stulli* and *nigriventris*, these taxa are not included. From large to small, the forms may be thus arranged: *haetianus, stejnegeri,* and *canus*; *maculatus* and *greenwayi, jamaicensis, barbouri, curtus* and *androsi,* and *pardalis.* Of the three forms which are poorly represented, *pilsbryi* appears to be small, *stulli* moderate, and *nigriventris* large.

The tail length/total length ratio has been computed for all specimens; there is little or no sexual dimorphism in this character, and ratios for both sexes have been combined. In the complex, this ratio (X 100) varies from 9.4 to 16.5, in individual specimens. Averages for taxa vary between 10.7 and 13.7. Ranking the taxa from relatively short to relatively long tail yields the following series: *canus, jamaicensis, stejnegeri, stulli, greenwayi, maculatus, pilsbryi, barbouri, pardalis* (Cuba), *androsi, nigriventris, haetianus, curtus, pardalis* (Isla de Pinos), and Bimini snakes with the highest ratio. Comments on the significance of these ratios will be made at appropriate places later in this paper.

Scalation

The number of ventrals, subcaudals, pre- and post-oculars, supra- and infralabials, scale rows, and presence or absence of parietal contact have been variously used by workers to define and differentiate the populations in the *pardalis-maculatus* complex. The presence or absence of keels on the dorsal scales has already been partially commented on, but will be discussed further below.

The number of ventrals varies between a low of 140 (Cuban *pardalis*) and a high of 208 (*maculatus*). Ranked by the average number of ventrals (both sexes included), the populations can be thus arranged in a series from low to high average number of ventrals: *pardalis* (Cuba), *pardalis* (Isla de Pinos), *curtus,* Bimini snakes, *nigriventris, greenwayi, barbouri, androsi, stulli, pilsbryi, canus* and *jamaicensis, haetianus, stejnegeri, maculatus.*

The number of subcaudals in the complex varies from a low of 22 (*barbouri*) to a high of 41 (*maculatus*). The lowest average number of subcaudals occurs in *nigriventris* (25.5), with both populations of *pardalis* and that of *barbouri* slightly higher (28.2

to 29.9). The highest average number of subcaudals occurs in *haetianus* (37.0), with *maculatus* only slightly lower (36.3). The remaining taxa are intermediate between these extremes.

The number of preoculars is typically 1/1 in the entire assemblage of forms. Counts of 2/1 and 2/2 occur rarely, and all large lots of material invariably show a few individuals with these abnormal counts (three out of ten *androsi*, two out of 15 *barbouri*, one out of 20 *canus*, two out of 67 *pardalis*, etc.). The number of postoculars is likewise variable; here however, there seems to be a definite tendency within a population toward either 2/2 or 3/3 postocular scales. For example, Cuban *pardalis* usually have 2/2 postoculars (42 of 57 specimens), *maculatus* usually has 3/3 (15 of 17 specimens), *canus* usually has 3/3 (17 of 20 specimens). Counts of 2/3 are not common but do occur; abnormally, there is one *haetianus* with 3/5 and one boa from Bimini with 3/4. Of the specimens of *haetianus*, one (ANSP 10279) has a complete row of suboculars separating the eye from the supralabials, and another (USNM 75925) has a single subocular scale. Two specimens of *stulli* (MCZ 44871-72) both have a single subocular. These four snakes are the only specimens examined with subocular scales.

Supra- and infralabials are variable; the number of the former is usually 9/9 or 10/10, but occasional specimens have 8, 11, or 12 on one or both sides, and all combinations from 8 to 12 may occur. Infralabials likewise vary from 9/9 to 12/12, with an occasional 13 unilaterally. Neither supra- nor infralabials are useful, in our opinion, in defining or differentiating populations.

The number of scale rows at midbody is another character which varies within populations, and only tendencies can be pointed out. In any considerable series from a population, at least two counts occur, and sometimes three. In general, the forms may be said to be characterized by the following number of scale rows at midbody, although it must be remembered that there are exceptions in every case:

23 scale rows — *pardalis*, *canus*, *curtus*, *nigriventris*
25 scale rows — *maculatus*, *stulli*, Bimini, *androsi*, *barbouri*, *greenwayi*
27 scale rows — *stejnegeri*, *haetianus*

The populations of *jamaicensis* and *pilsbryi* cannot be categorized; of four specimens of *pilsbryi*, each has a different midbody count — 23, 24, 25, 27. Probably this form belongs to the 25 scale-row group. Of nine *jamaicensis*, four have counts of 25, three of 27, one of 26, and one of 29; this form probably belongs with the 27 scale-row group.

As far as parietal contact is concerned, as with all other scale characters, this one is also variable. When any sizable series is studied, usually some specimens will have the parietals in contact and others will not. The only major exception to this statement is that all 15 specimens of *barbouri* examined lack parietal contact. The general tendency is, however, for all members of the group to lack parietal contact; exceptions to this statement are Isla de Pinos *pardalis*, *haetianus*, and *greenwayi*. These three populations have more individuals with the parietals in contact than without contact; in fact, *greenwayi* was partially diagnosed (Barbour and Shreve, *op. cit.*:2) on this basis. However, as in other members of the group, the Bahaman forms *canus* and *curtus* show some individuals with the parietals in contact, and it is probable that when other specimens of *greenwayi* are collected some will show lack of contact between the parietals.

The use of carination of dorsal scales as a character in separating the "*pardalis*" and "*maculatus*" groups has been made previously, and attention was then drawn to the variability of this character within populations. Those taxa which show a tendency toward smooth scales include: *pardalis*, *jamaicensis*, *stulli*, *haetianus*, Bimini snakes, *greenwayi*, and *nigriventris;* whereas *maculatus*, *pilsbryi*, *stejnegeri*, *canus*, *curtus*, *androsi*, and *barbouri* have more individuals with keeled than with smooth scales. It should be kept in mind that these are tendencies only, and in any large series from the same general locality individuals may be found with keeled or smooth scales.

Pattern

All members of the *pardalis-maculatus* complex are distinguished from the other West Indian members of the genus by having a tan to brown dorsum with a series of many, more or less prominent, darker blotches from the occiput to the tail. A constant feature among the forms is the presence of paired blotches on the venter; these may be large and conspicuous as in *pardalis* (Fig. 1) and *nigriventris* (Fig. 2), or much restricted and almost absent as in *stulli* (Fig. 3). Including these two ventral rows, there are from six to twelve longitudinal rows of blotches or spots in the complex. Again, as with the other characters already treated, within populations the number of rows is not constant if large series are examined. The only major exception to this statement is that nine of the ten *androsi* examined had 10 rows of blotches (one was indeterminate). The largest variation in number of rows is in the series of 17 specimens from Bimini; here, counts of 8, 9, 10, 11 and 12 rows were encountered, with 10 rows being the most frequent. The populations of *canus* and *maculatus* are also rather variable, the former having counts of 6, 7, 8, 9 (6 rows most frequent), and the latter 6, 8, and 10 (8 rows most frequent).

Basing our conclusions on the frequency of occurrence of number of rows in samples examined, we would categorize the following taxa by rows of blotches as follows:

6 rows — *pardalis* (Cuba), *canus*
8 rows — *pardalis* (Isla de Pinos), *maculatus, pilsbryi, stejnegeri, nigriventris*
10 rows — *stulli, jamaicensis, haetianus, curtus*, Bimini snakes, *androsi, barbouri*

In the above summary, *greenwayi* is not included; the two specimens at hand have 8 and 10 rows of blotches. The much faded *stulli* was diagnosed by Grant (1940:8) as having only two rows of dorsal spots; this is true anteriorly, but posteriorly the complete complement of 10 rows of blotches can be determined.

The distinctness of the blotches varies both between and within populations. In some forms (*maculatus*, Fig. 4) the blotches stand out boldly against a much paler ground color which in general lacks accessory interblotch dark pigment. In others, such as *pardalis* and some of the Bahaman populations, the blotches are less distinct. Coupled with this is the prevalence in the Bahaman forms (*canus, curtus, androsi, barbouri*, but not necessarily *greenwayi* of which no juveniles and only two adult males are known) of a radical ontogenetic change in pattern. In these forms, the juveniles are heavily and profusely spotted with dark gray to brown blotches on a lighter ground color (Fig. 5); these spots become increasingly less prominent with age and adults of both sexes are often but faintly spotted, the spots being much restricted and small (Fig. 6), or are completely unicolor tan to brown with no indication of spotting present. Such ontogenetic change does not occur in any of the other forms of which juveniles are known (*pardalis, maculatus, pilsbryi, haetianus*); in these forms the adult and juvenile patterns are identical.

The number of blotches in the paramedian longitudinal rows range in the complex from a low count of 25 (Cuban *pardalis*) to a high of 90 (Bimini). In no instance can two forms be separated on the basis of number of blotches, although the size and extent of the blotches are often diagnostic. For example, the three Cuban forms (*pardalis, maculatus, nigriventris*) have blotch counts which overlap: 25-42 in *pardalis*, 33-54 in *maculatus*, 37-46 in *nigriventris*. However, inspection of a specimen of each of these snakes leaves no doubt as to which taxon it represents. In *pardalis* the blotches are large and dark, closely approximated, and relatively not prominent; in *maculatus*, the blotches are medium sized and very dark against a light ground color, and in *nigriventris* the blotches are small, appear to be more numerous and somewhat more crowded together and are not prominent, much as in *pardalis*.

The two ventral rows of blotches are usually far more prominent posteriorly than anteriorly; the extreme of this condition is shown by *stulli* where there is only the faintest indication of ventral spotting posteriorly, and the belly is almost immaculate anteriorly. The most prominent ventral blotches are in *pardalis* and *nigriventris;* in the latter the blotches may be so large as to be confluent, producing an almost black belly in some specimens.

Stull (*op. cit.*) and later Bailey (*op. cit.*) used the color of the tip of the tail as a feature to differentiate the various forms of the *pardalis* complex in the Bahamas. In general, the Bahaman populations have pale tails or tails which are unicolor with the dorsal ground color while they are young, and the dorsal surface of the tail becomes increasingly dark with age, in some instances olive green and in others dark brown to black. Often only the dorsal surface is affected, but in some individuals the entire distal portion of the tail may be involved. We have checked the tail color on all specimens, and the following remarks are based on the tail color of adults only (in juveniles the tail is almost uniformly pale or only as dark as the dorsal ground color). In only six populations is the tail more often light than dark: *pardalis* (both Cuba and the Isla de Pinos), *maculatus*, *jamaicensis*, *stulli*, *stejnegeri*, and *greenwayi*. Of *stulli* and *greenwayi* we have seen only two adults each and three adult *stejnegeri*, and consequently these data may be inaccurate. Of all adult *pardalis* examined (54), only two Cuban individuals have dark tails; of 14 adult *maculatus*, four have dark tails. The forms *haetianus*, *canus*, *curtus*, *androsi*, and *barbouri* more often have dark tail tips, but pale-tailed individuals of each of these populations have been examined. Too few *pilsbryi* and *nigriventris* are known; two adult specimens of each were studied and in each case one has a dark and the other a light tail.

The presence of pale occipital spots has been used to distinguish various taxa in the group under consideration. In the Bahaman forms (*canus*, *curtus*, *androsi*, *barbouri*, *greenwayi*) no specimen of the 77 examined shows any indication of these spots. Neither do they appear in any specimen of *nigriventris*, *haetianus*, *stulli*, *jamaicensis*, or *maculatus*. In all specimens of *pilsbryi*, *stejnegeri*, and Isla de Pinos *pardalis*, the spots are present; they are a constant and bold pattern feature of *pilsbryi*. Only in Cuban *pardalis* are there individuals with and without occipital spots; 29 adults lack them and 18 adults possess them.

The other pattern feature which is restricted to the Bahaman group of forms is the presence of an anterior dark line extending from the posterior margin of the eye posteriorly along the body for a variable distance along the seventh or eighth scale row, and gradually becoming fragmented to form the second (counting the paramedian row as the first) of the dorsal rows of longitudinal spots. This longitudinal line is apparent in all the Bahaman forms except *greenwayi*, whose dorsal coloration and pattern is perhaps the most unorthodox of the entire assemblage of the *pardalis-maculatus* groups.

Proposed arrangement

It should be obvious from the foregoing comments that the present arrangement of trivial names needs serious revision. Characters which previously have been used to separate major groupings within this section of the genus have been demonstrated to be inadequate or invalid. Reliance upon carination of scales to distinguish between *species* is improper; in fact, almost all characters of squamation appear to be sufficiently variable as to cause confusion. Of all the characters used, we feel that coloration and pattern, combined with characters of scutellation (provided these are used with discretion and with the frank admission from the outset that we are dealing in many cases with trends and tendencies and not hard and fast categories), and overall size, appear to give the most satisfactory results for separating and combining the thirteen named forms into a more realistic and sound arrangement.

Analysis of species by geographic areas

We have arranged the various taxa by geographic areas, and discussion of the variation and relationships of the snakes in each of these areas follows.

The Bahamas. The five forms currently known from the Bahamas are as follows, with their respective ranges.

androsi — Andros Island and Mangrove Cay
barbouri — Long Island; Eleuthera Island; South Eleuthera Island; Warderick Wells Cay; Cat Island
canus — Great Inagua Island
curtus — New Providence Island
greenwayi — Ambergris Cay, Caicos Island

In addition we have examined 17 specimens from the Bimini Islands (AMNH 73501-04, 73542, 73708, 75414-18, 75623, 76870-71, 68818; UMMZ 110869-70) and one (USNM 81536) from Doubleheaded Shot Cay which lies on the Cay Sal Bank between southern Florida and the northern coast of Cuba. Comments on these 18 specimens will be made below.

With the exception of *greenwayi*, the remaining four forms (plus the Bimini and Cay Sal specimens) are closely related and have many features in common. Among these features are: moderate size (males no larger than 408 mm., females 373), tail color usually dark in adults, complete absence of occipital spots, usually 10 rows of body blotches, parietal contact usually absent, dorsal scales usually keeled, postoculars more often 3/3, and scale rows either 23 or 25 at midbody. Ventrals range from 146 to 183, subcaudals from 22 to 37. In addition, these snakes have distinctly different juvenile and adult patterns as previously pointed out (Bailey *op. cit.*:48, had commented on the differences between juvenile and adult coloration and pattern), and have the longitudinal line along the anterior sides, a feature which is present in no other forms.

Of the four, *canus* can be distinguished from both *curtus* and *barbouri* by its higher (170-183) ventral count (149-157 in *curtus;* 154-165 in *barbouri*) and six rows of blotches; *androsi* differs from *curtus* in number of ventrals as well (157-173 in *androsi*). The number of scale rows at midbody, and ten rather than six rows of blotches distinguish *androsi* from *canus;* the former usually has 25, the latter always 23. The number of scale rows distinguishes *barbouri* from *curtus;* the former usually has 25, the latter usually 23. The forms *barbouri* and *androsi* are very close; although the number of ventrals overlap, the means are different (164.0 in *androsi*, 158.3 in *barbouri*). The tail is relatively shorter (10.7%) in *canus* than in any of the other Bahaman forms.

On the other hand, *greenwayi* is so distinctly different not only from the above Bahaman populations, but from all other members of this group (and from *melanurus* and the *semicinctus* assemblage as well), that its affinities are questionable. Whereas the other Bahaman snakes are typically pale tan with rather restricted dorsal blotches, both dorsally and ventrally, *greenwayi* is extremely dark. The blotches are very large and extensive, and with irregular edges; often adjacent spots in different rows are indiscriminately fused, and the brown interspaces are much stippled with black (Fig. 7). The ventral rows of blotches extend to the throat. The head itself is stippled black and white, giving a salt-and-pepper effect. There is no indication of the anterior lateral longitudinal line which is so characteristic of the other Bahaman snakes. The number of ventrals (157-158) falls within the range of *barbouri*, just above the range of *curtus*, and much below the range of *canus*. The supposedly diagnostic feature of absence of parietal contact may not necessarily be valid, since this character appears in, of the other Bahaman forms, at least *canus* and *curtus*. The smooth dorsal scales of *greenwayi* differ from the usually keeled scales of *canus*, *curtus*, *androsi* and *barbouri*; each of these (except *androsi*) does however occasionally have smooth scaled individuals. In having 25 scale rows, *greenwayi* resembles *androsi* and *barbouri*, but differs from the typically 23 scale-rowed *canus* and *curtus*. The latter however does have some 25 scale-rowed individuals. In summary, we feel that *greenwayi* is sufficiently distinct in coloration and pattern that it should not be regarded as closely related to the other Bahaman *Tropidophis*, and consequently we regard it as a separate species.

The 17 snakes from the Bimini Islands are also remarkable. At the time of Stull's revision, apparently there were no *Tropidophis* known from these islands; insofar as we know, the report of Hecht and Walters (1955) was the first recording of this genus from Bimini. These authors gave an excellent description of the ontogenetic changes involved in the Bimini snakes, and called them only *T. pardalis;* they compared them with the other Bahaman snakes, but left the question of subspecific determination unanswered. Unfortunately, the situation is not any clearer at present, despite the acquisition of additional material. The Bimini snakes have ventral counts of 140 to 160 (mean 153.8), and are thus closely comparable to *curtus* (range 149-157, mean 151.8). Nine of the 17 are juveniles. However, both males and females apparently reach a larger size than *curtus;* the largest male *curtus* is 330, the largest male Bimini snake is 359, whereas the largest female *curtus* is 310, and the largest Bimini female is 362, with an incomplete tail. Ratio of tail length/total length is approximately the same in the two groups. Both usually have dark tails, always lack occipital spots, usually have 10 rows of blotches, lack parietal contact, and have approximately the same range of subcaudals. They differ most strikingly in three characters: the Bimini snakes usually have smooth rather than keeled scales, usually have 3/3 rather than 2/2 postoculars, and usually have 25 rather than 23 scale rows. None of these characteristics is definitive, however, and each population has characteristics of the other.

The herpetofauna of the Bimini Islands has been discussed by Oliver (1948); the amphibians include *Hyla septentrionalis* and *Eleutherodactylus ricordi planirostris* (both of which are rather widely distributed in the West Indies and Florida), and the reptiles are: *Sphaerodactylus notatus* (which is also widely dispersed), *Anolis carolinensis lerneri*, *A. distichus biminiensis*, *A. angusticeps chickcharneyi*, and *A. sagrei ordinatus.* Three of the anoles (*lerneri, biminiensis, chickcharneyi*) are restricted to the Biminis, whereas *ordinatus* is more widely distributed (Turk's Island to New Providence, Barbour, 1937:126). Of the four anoles, three (*angusticeps, carolinensis, sagrei*) are Cuban in origin and affinities, and one (*distichus*) is Hispaniolan. From these remarks it is apparent that: 1) the Bimini herpetofauna is derived from two sources, Cuba and Hispaniola, and 2) at least in some forms differentiation into distinct subspecies has occurred on the Biminis. The boas of Bimini are related neither to the Cuban nor to the Hispaniolan *Tropidophis*, at least closely; their affinities are distinctly with the remainder of the Bahaman complex. It also appears that some differentiation from the remainder of the complex has also taken place, but that this has not progressed sufficiently far, at least in our opinion, to be nomenclatorially recognized.

The Bimini *Tropidophis* are most closely related to *curtus.* Bimini and New Providence, where *curtus* is known to occur, are separated by some 130 miles of ocean; lying between these two islands is the much larger Andros Island, which is inhabited by the distinctly different *androsi.* All these islands are part of the Great Bahama Bank. The significance of this peculiar distribution of *curtus* remains unknown; it is probable that *curtus*, as here delimited, represents two distinct entities which fortuitously are genetically very similar. In the absence of any concrete differences between the two populations, we have no choice but to regard them both as *curtus.*

One other Bahaman specimen requires comment. This is a juvenile female (USNM 81536) from Doubleheaded Shot Cay, on the Cay Sal Bank. This specimen represents the westernmost occurrence of the Bahaman group of snakes; the snake was originally reported (Cochran, 1934:46) as *T. pardalis pardalis,* but Bailey (*op. cit.*:50) later commented that it "has the typical coloration of Bahaman juveniles." Its 159 ventrals eliminate only *canus* from consideration; this number lies within the known range of ventrals of *curtus, androsi, barbouri,* and *greenwayi,* although we doubt strongly that it is related to the geographically remote and extremely distinct latter form. It is useless to speculate further upon the identification of this snake since there is nothing distinctive about it which will facilitate allocation. We wish merely to point out that there apparently is a population of *Tropidophis* with distinctly Bahaman (rather than Cuban) affinities on the Cay Sal Bank.

It may be wise to point out here that the name *Ungualia curta* Garman was based on a specimen reportedly from Cuba. Stull, with justification, regarded this provenance as "probably erroneous" (*op. cit.*:31). It will be shown later in this paper that there is a single specimen of the Bahaman group of snakes known from Cuba, and it is entirely possible that Garman's type was indeed Cuban in origin. Should this prove to be the case, it may well be that certain shifting in the nomenclature of this entire lot of snakes will be necessary.

In summary, we consider the Bahaman snakes to represent two species, not closely related to any of the other West Indian small boids, and not closely related to each other. One of these is composed of four recognizable subspecies, and the prior name for this group is *canus* Cope, 1868. In our opinion, the *Tropidophis* of the Bahamas should be designated as follows:

Tropidophis canus canus Cope, 1868
Tropidophis canus curtus Garman, 1887
Tropidophis canus androsi Stull, 1927
Tropidophis canus barbouri Bailey, 1937
Tropidophis greenwayi Barbour and Shreve, 1936

Jamaica. Our comments on the Jamaican *Tropidophis* are hampered by the extreme paucity of specimens in American collections. We have seen only 16 specimens from the island representing the three known forms; remarkably, three of these are erythristic, and are the only such individuals we have seen from anywhere in the West Indies. The three forms known from Jamaica are, with their distributions:

jamaicensis — south slope
stulli — Portland Point
stejnegeri — north slope

Considering these snakes together, they share certain characteristics and have others which are quite distinctive. All are moderately sized snakes; *stejnegeri* reaches the largest size (416 in males, 352 in females). All have low tail/total length ratios (11.0-11.6). All have parietal contact and usually 3/3 postoculars, and the scale rows are either 25, 27, or 29. The number of rows of blotches is either 8 or 10, and a pale tail is more common than a dark one, although both *jamaicensis* and *stejnegeri* show the dark tail tip at times. Of the three, *stejnegeri* is most strikingly different. It alone has large occipital spots and has keeled dorsal scales; both *stulli* and *jamaicensis* lack spots and have smooth dorsals. The three forms are completely separable on the basis of number of ventrals: *stulli* has from 166 to 167 (166.5), *jamaicensis* from 169 to 178 (174.3), and *stejnegeri* from 184 to 187 (186.0).

The major problem with these three forms is their interrelationships. Stull (*op. cit.*:12) described *jamaicensis* as a race of *maculatus;* later Grant (1940:157) described *stulli* as a race of *maculatus* and *stejnegeri* as a race of *pardalis.* The early brief descriptions of Grant's new subspecies were later expanded (Grant, 1941b:119-122). In the light of our data, it is at once obvious that the association of the name *stejnegeri* with *pardalis*, and of *jamaicensis* and *stulli* with *maculatus* is incorrect. The supposition that *pardalis* has keeled scales and *maculatus* smooth scales is not correct, as has been mentioned earlier; in fact, the reverse is more or less true. Thus *jamaicensis* and *stulli* might more properly have been regarded as subspecies of *pardalis*, and *stejnegeri* of *maculatus*. Such a course has even less to recommend it than the former allocation. As far as we are concerned, the Jamaican snakes are not at all closely related to the Cuban *pardalis* and *maculatus*, and are far more closely related *intra se* than to these Cuban snakes. If relationship with Cuban snakes must be sought, then the Jamaican snakes as a group are more closely related to *maculatus* than *pardalis*, but this relationship is not close nor is it on a subspecific level. From *pardalis*, the Jamaican snakes differ in much larger size, relatively shorter tails, usual absence of occipital spots (although *stejnegeri* and some Cuban and all Isla de Pinos *pardalis* have them), 8 or 10 rows of blotches (usually 6 in Cuban, 8 in Isla de Pinos *pardalis*), 3/3 rather than 2/2 postoculars, and 25, 27, or 29 scale rows (usually 23, occasionally 25, and never 27 or 29 in *pardalis*), and more ventrals. From *maculatus*, the Jamaican snakes differ in somewhat larger size and definitely more robust build, relatively shorter tail, smooth rather than keeled scales (although the scales are keeled in *stejnegeri* and smooth in some *maculatus*), and less ventrals and subcaudals. For reasons advanced later, we regard the Jamaican snakes as all belonging to one species, along with boas from other areas, and we withhold for the moment any use of trinomials. Certainly there is no question of the distinctness of the three Jamaican forms from one another.

Hispaniola. Only a single form, *haetianus*, has been recorded from Hispaniola (Stull, *op. cit.*:14-18; Cochran, 1941:325-329). In addition to occurring on the main island, this snake is known as well from Ile Tortue and Gonave Island. Cochran has discussed at some length the variation in coloration, pattern, and scutellation in *haetianus*, and little need be said concerning these matters here.

Comparing *haetianus* with the other West Indian snakes reveals that it is not closely related to the Bahaman *T. canus;* it differs in reaching a much larger size (*haetianus* is the largest member of the complex), usually has the parietals in contact, usually has the dorsals keeled (true as well only of *c. curtus* from Bimini, but occurring sporadically in the other Bahaman subspecies except *androsi*), and scale rows usually 27 (the type of *haetianus* is unique in having 29 scale rows), a count that has never been observed in any population of *T. canus*. In addition, *haetianus* lacks the change from juvenile to adult patterns and the longitudinal lateral dark line of the Bahaman snakes.

The association of *haetianus* with *maculatus* we regard as erroneous. The main difference is the presence of smooth scales in *haetianus* in contrast to keeled scales in *maculatus*. Also, *haetianus* reaches a much larger size, has a relatively longer tail, usually has a dark rather than light tail tip, has 10 rows of blotches (Fig. 8) rather than 8, usually has parietal contact, and has 27 rather than 25 scale rows. The number of ventrals is lower than in *maculatus*, but there is overlap between the two populations. The style of patterns is different in the two forms. In *maculatus* the blotches are prominent and dark on an almost clear ground color; in *haetianus* the pattern is diffuse, obscure, and indistinct since the ground color is much stippled and dusky in the interspaces. The Hispaniolan snakes are, in addition, much more robust than *maculatus*.

The closest affinities of *haetianus* appear not to be with either of its two Cuban relatives, but rather with the snakes of Jamaica. Both *haetianus* and the Jamaican forms are relatively large and robust, both usually lack occipital spots, have 8 or 10 rows of blotches, usually are smooth scaled, have 3/3 postoculars and have 25, 27, or 29 scale rows. The basic patterns are very similar, although this pattern is much obliterated in *stulli*. Differences between them include relatively longer tail in *haetianus*, usually dark tail in *haetianus*, and usually parietal contact in *haetianus*. The range of ventrals in *haetianus* is comparable to that in the aberrant *stejnegeri* (180-192, mean 185.2 in the former; 184-187, mean 186.0 in the latter). The similarities between the Hispaniolan and Jamaican snakes outweigh, in our opinion, their differences; we are placing special emphasis on the similarity of patterns in the populations involved. For these reasons we regard the snakes of Jamaica and Hispaniola as belonging to one species, and the names may stand as:

Tropidophis haetianus haetianus Cope, 1879
Tropidophis haetianus jamaicensis Stull, 1928
Tropidophis haetianus stulli Grant, 1940
Tropidophis haetianus stejnegeri Grant, 1940

Cuba and the Isla de Pinos. More forms of the *pardalis-maculatus* complex occur in Cuba than on any other island of the West Indies; the situation has been made even more complicated by the fact that several of the forms (especially *maculatus*) have been poorly represented in American collections. Fortunately, this situation has been somewhat remedied, although inadequate material still makes certain problems unsolvable. The forms which have been known to occur on Cuba are:

pardalis — widespread and on the Isla de Pinos
maculatus — western Cuba and Isla de Pinos
pilsbryi — central and eastern Cuba
nigriventris — west central Cuba

Unaware of the possible diversity of Cuban *Tropidophis* at the time of her revision, Stull confused several specimens and forced them into either *maculatus* or *pardalis*. This situation was partially remedied with Bailey's description of *pilsbryi* and *nigriventris*, but the picture was still not complete. We know that our contribution here is not the final word, but certain peculiariies and discrepancies can now be clarified.

The most widespread of the Cuban multispotted boas is *pardalis*, which occurs from one end of the island to the other (although it is still unknown from extreme eastern Oriente), and on the Isla de Pinos as well. We will discuss the Cuban and Isla de Pinos populations as two entities, since there are certain striking differences between them. In Cuba, *pardalis* is a moderately sized snake, the smallest of the entire complex; males reach at least a maximum size of 343 (tail incomplete), females 292. The tail is relatively short (12.9% in tail/total length ratio). The tail color in adults is usually pale (45 of 47 individuals), the occipital spots are usually absent in adults (30 of 48 snakes), but may be present in juveniles, blotch rows are usually 6 (8 rows occur in four of 55 specimens), there are few dorsal spots in the paramedian rows (25-42), the parietals usually do not touch, the scales are almost always smooth, there are usually 2/2 postoculars (42 of 57 specimens), there are usually 23 scale rows (although counts of 21, 22, 24 and 25 occur), and the number of ventrals is low (140-165). The heavily blotched venter will distinguish *pardalis* from all other West Indian *Tropidophis* except *nigriventris*. The low number of ventrals will separate *pardalis* at once from *maculatus* and *pilsbryi*, although the latter is represented by an individual with 160 ventrals, just below the highest count of *pardalis* (165). Comparison with *nigriventris* is made below.

The Isla de Pinos *pardalis* agree with the Cuban population in moderate size, having light tail tips, smooth dorsals, usually 23 scale rows at midbody, and comparable numbers of ventrals and subcaudals. They differ in always having occipital spots in both adults and juveniles, more often having 8 rather than 6 rows of blotches, more often having parietal contact, and more often having 3/3 postoculars. In combination these characters might justify the erection of a new taxon for the Isla de Pinos snakes. We are reluctant to do so because of the great overlapping of the characters; none is completely definitive, and all are matters of degree. In the following comparisons with other Cuban material, we will disregard the Isla de Pinos snakes, although well aware of their similarities and differences with reference to the Cuban populations.

Not included in the above discussion are a series of *pardalis* (ANSP 10251-56, 10280) with locality data "Cuba"; the first lot of these was collected by Felipe Poey, the single specimen apparently not by him. Of the series, two (ANSP 10254-55) have prominent occipital spots, and the former has 3/3 postoculars as well. It would not be surprising if these two snakes were actually from the Isla de Pinos; we know that Poey visited the Isla with Don Carlos de la Torre (Conde, 1958:221), and it is not impossible that these two snakes were collected there. Since there is doubt thus cast upon the entire lot, we have not utilized any data from this material in our computations and calculations.

Most closely related to *pardalis* is *nigriventris*. However, we do not regard this relationship as a subspecific one; both forms occur in the provinces of Las Villas and Camagüey. We have specimens which indicate that the two are precisely sympatric; in Las Villas, *pardalis* is known from Cumanayagua, Soledad, and Trinidad, and *nigriventris* from Trinidad as well. The only specimen of *pardalis* from Camagüey is from Paredón Grande, a key northeast of Cayo Romano, whereas *nigriventris* is known in Camagüey from the southeastern portion of the province, in the Martí-Camagüey city area. There are no specimens of *nigriventris* from Oriente where it may be expected, and we have seen only five specimens of *pardalis* from Oriente, all from San Germán in the central portion of the province. Specimens of *pardalis* from the Trinidad area have the highest ventral count of any examined, and Trinidad *nigriventris* have high counts as well; thus in southern Las Villas the two species are very close. It may be considered that the relationship is a subspecific one on this basis, but we are reluctant to assume so.

Based on a small sample of five snakes, *nigriventris* is seen to reach a larger size than *pardalis* (female *nigriventris* reach at least a size of 355 mm., and males 351 mm., both specimens in question having incomplete tails), but in all scale counts the two species are very close. Both lack occipital spots, lack parietal contact, have smooth dorsals, and have 23 scale rows. Of two adult *nigriventris*, the tail is dark in one and pale in the other; 2/2 postoculars occurs with more frequency (3 snakes) than 3/3 (2 specimens). Few Cuban *pardalis* have 8 rows of blotches; all *nigriventris* examined have 8 rows, although the two Las Villas specimens have the lowermost dorsal rows obsolete. The number of blotches in the paramedian rows varies between 25 and 42 in *pardalis*, and between 37 and 46 in *nigriventris*. Thus the latter form has a few more blotches on the average than *pardalis*, but the counts overlap greatly. The major differentiating feature of the two snakes is the much smaller head of *nigriventris;* if specimens of the two taxa are compared, the smaller head of *nigriventris* is immediately apparent. The extent of the medial fusion of the ventral blotches, giving an almost entirely black belly, is too variable in *nigriventris* to be an absolute character; the two Las Villas specimens (USNM 138512, 138510) have ventral blotches which are less prominent and extensive than many *pardalis.*

Comparison of *nigriventris* with *maculatus* is almost unnecessary. The dark ground color and less conspicuous dorsal blotching of the former stand in direct contrast to the light ground color and conspicuous pattern of the latter. The head of *maculatus* is not strikingly small, and *maculatus* usually has keeled rather than smooth scales. The number of ventrals will also separate the two populations (144-170 in *nigriventris*, 189-208 for *maculatus*).

The form *pilsbryi* was described by Bailey (*op. cit.*:42) on the basis of three specimens, an adult male and two juvenile females, all of which we have examined. These snakes are from two widely separated areas — the Sierra de Trinidad in Las Villas, and the Guantánamo Basin and Miranda in central and eastern Oriente. The most obvious feature of *pilsbryi* is the occurrence of one or a pair of light occipital spots which, in the type, stand out boldly against the dark brown background. In the original description, Bailey (*op. cit.*:43) commented on two other Oriente specimens which he did not consider as being *pilsbryi;* these are USNM 27455 and 12361. We have examined both of these snakes; there is no reason to exclude USNM 12361 from *pilsbryi.* It is from "eastern Cuba" and thus within the known range of the form, and, although the occipital spots are rather faint and the ventral count is four scales lower than those of the type and paratypes, it can very appropriately be considered *pilsbryi.* As for USNM 27455, we agree with Bailey that this snake, also from "eastern Cuba," is definitely not *pilsbryi*, nor is it *pardalis,* to which Stull (*op. cit.*:28) assigned it. It will be discussed in detail below.

Aside from the presence of occipital spots (which condition *pilsbryi* shares with some Cuban *pardalis,* but in which form the spots are never so bold or prominent), *pilsbryi* differs from *pardalis* in smaller size (maximum, a male, 212); usually 8, occasionally 10, rows of blotches; keeled dorsals; 3/3 postoculars;

scale row counts of 23, 25, and 27 (*pardalis* usually has 23, but may have 25); and higher ventrals (140-165 in *pardalis*, 160-178 in *pilsbryi*). From *nigriventris*, *pilsbryi* differs in having prominent occipital spots, being smaller, having a relatively longer tail, having keeled scales, and a greater number of ventrals. Both snakes may have dark bellies with rather prominent blotches (Fig. 9), but this feature is more conspicuous in *nigriventris* than in *pilsbryi*.

The name *maculatus* has been applied to moderately sized, laterally compressed snakes from western and central Cuba. Cochran (1941:327) applied this name to USNM 27455, from "eastern Cuba," but this designation is not correct. There is in addition one *maculatus* (MCZ 12455) from the Isla de Pinos. As a group, the *maculatus* differ from all other Cuban snakes in their much higher ventral count (189-208); there is no overlap in this character with any other discovered Cuban form (see, however, the discussion below). Only *pilsbryi* has keeled dorsals as frequently as does *maculatus*; *nigriventris* and *pardalis* are usually smooth scaled. The coloration and pattern of *maculatus* sets it off as well from all other Cuban snakes, as has been pointed out previously, and little confusion should result in identifications. Comparisons of *maculatus* with the other Cuban multispotted *Tropidophis* has been made in the above paragraphs.

The problem with the Cuban snakes is not one of whether these four named forms are distinct; this is eminently so. The question is, rather, what is the relationship of these snakes to one another, and to the remainder of the West Indian small boas as well? As far as we are concerned, the four Cuban snakes merit specific, rather than any combination of subspecific status. Of the four, *pardalis* and *nigriventris* are related; *maculatus* and *pilsbryi* are likewise related. But the former pair is apparently sympatric (or possibly the range of *nigriventris* is surrounded by that of *pardalis?*), and the resemblances may well be superficial. The latter pair are widely separated geographically; that *pilsbryi* may be more common than now known is indicated by the statement of Alayo (1951 :108) that *Tropidophis* sp. with (translated) "a large white spot on either side of the neck" were taken at Santiago de Cuba. Some 250 kilometers separate the easternmost station of *maculatus* (Managua, Habana Province) from the westernmost station of *pilsbryi* (Mina Carlota, Las Villas). Although these two snakes show some resemblances to one another (both have 8 rows of blotches, lack parietal contact, have keeled dorsals, 3/3 postoculars), the much smaller known adult size of *pilsbryi* as well as the extremely prominent occipital spots (a feature which is never demonstrated in *maculatus*) and the dark rather than light ground color, make it seem more satisfactory at present to regard these snakes as belonging to distinct species.

As far as extra-Cuban relatives of each of the four Cuban populations is concerned, we feel that none has a close relative elsewhere. Certainly the formerly current tendency to call the Bahaman snakes all races of *pardalis* is extremely misleading; no two snakes could be more different than *pardalis* and *androsi*, for example. None of the Jamaican or Hispaniolan snakes is related so closely to *pardalis* as is *nigriventris*. The only non-Cuban West Indian *Tropidophis* which has anything approaching the occipital spots of *pilsbryi* is the Jamaican *stejnegeri*, and close relationship between these two snakes is improbable. We have already commented on the distant possibility of close relationship between *maculatus* and *T. haetianus*, but this too has been discarded. Insofar as we are concerned, each of the named Cuban forms should stand as a separate species, as follows:

Tropidophis pardalis Gundlach, 1840
Tropidophis maculatus Bibron, 1840
Tropidophis pilsbryi Bailey, 1937
Tropidophis nigriventris Bailey, 1937

We take this radical action with full knowledge that additional material may prove relationships at present unguessed between these four snakes; we do not doubt that there are grounds for others to challenge our separating these four species from the remainder of the West Indian multispotted boids nomenclatorially. Of the four, the relationship of *T. pardalis* and *T. nigriventris* is the closest, and future collections may reveal that the two are subspecifically related.

There are four specimens of *Tropidophis* from Cuba which have caused endless confusion to ourselves and to other workers as well. These snakes are:

AMNH 2946 — Nuevitas, Camagüey
USNM 27455 — eastern Cuba
MCZ 47896 — Guardalavaca, Banes, Oriente
USNM 137084 — Soledad, Cienfuegos, Las Villas

Of these four, AMNH 2946 is extremely interesting. This snake was called *T. p. pardalis* by Stull (*op. cit.*:28), but it certainly is not this species. In coloration, scalation, and markings, this snake belongs to the Bahaman assemblage, and is thus correctly assigned to *T. canus*. It is a young female, 195 mm. in total length, which possesses the adult pattern; the tail is pale, there is no parietal contact, the preoculars are 2/2, postoculars 3/3, the dorsals are keeled, there are 25 scale rows at midbody, 10 rows of blotches, and 48 and 51 blotches in the paramedian blotch rows on each side. The low number of ventrals eliminates only *T. c. canus* from further consideration; no other character or combination of characters will make it possible to assign this specimen to one of the three remaining subspecies of *T. canus*. An intriguing possibility is, of course, that this specimen represents true *Ungualia curta* Garman, originally described from Cuba. Geographically, certainly, one might expect a Bahaman species to occur in eastern, rather than western, Cuba. It is entirely possible that, with accumulation of additional *Tropidophis* from eastern Cuba, a population of *T. canus* will be discovered to occur in that area. Also Nuevitas is a seaport, and introduction of this single snake from New Province is not a remote possibility.

The remaining three snakes have had varied histories; only one (USNM 27455) is an old specimen. This snake was designated as *T. p. pardalis* by Stull (*op. cit.*:28), although she commented on the unusually high number of ventrals. Bailey (*op. cit.*:43) stated definitely that it is not *pilsbryi*. Cochran (1941:327) regarded it as *maculatus*. The two other specimens are more recently collected.

These three snakes (USNM 27455, MCZ 47896, USNM 137084) are very much alike and almost certainly represent the same form. Among them ventrals range from 178 to 191 (mean, 184.0), subcaudals 33 to 34 (33.5), two have dark tails and in the other the tail is light, occipital spots are absent in two and present in one, all have 10 rows of blotches, parietals are in contact in two and not in one, all have 3/3 postoculars, and scale rows are 25 in two and 26 in one. The tail/total length ratio is high (13.0-13.2, mean 13.1). These snakes are obviously closely related to *T. haetianus*, and may well represent a Cuban subspecies of the Jamaican and Hispaniolan snake in central and eastern Cuba. They are closest to *T. h. haetianus* in all characters, but are much smaller (largest female 244, largest *h. haetianus* 712), have keeled rather than smooth dorsals, and have 25 rather than 27 scale rows. The general style of pattern and pigmentation is comparable. As a group they have little in common with *pardalis* or *maculatus*, and likewise do not appear related to *pilsbryi* or *nigriventris*. We can merely point out at present that a representative of *T. haetianus* does occur in central and eastern Cuba; subspecific allocation must await further material, although for the moment these snakes seem most closely related to *T. h. haetianus*.

Discussion

The transition from the past concept of three species of *Tropidophis* in the West Indies (*pardalis*, *maculatus*, *nigriventris*), two of which were regarded as polytypic, to seven full species, five of which are monotypic, has been based on examination of considerably more material than has been available heretofore to other workers. Although the arrangement proposed here may seem a radical departure from the old system, we feel that it better expresses the relationships of the populations of these snakes in the West Indies. Taxonomy has a twofold duty, to express both differences and likenesses, and our arrangement tries to keep to a middle road in this regard. There has been a tendency in recent years to group together allopatric forms without due regard for factors other than their allopatry. In several instances, accumulation of additional material has shown such groupings to represent a complex of species, rather than an assemblage of subspecies.

It is not surprising that Cuba, the largest of the West Indian Islands, has the greatest variety of species of *Tropidophis*, not only in the *pardalis-maculatus* complex, but in the genus as a whole. As currently understood, the Cuban forms are: *T. pardalis*, *T. maculatus*, *T. pilsbryi*, *T. nigriventris*, possibly *T. canus* and certainly a representative of *T. haetianus*, and in addition *T. melanurus melanurus*, *T. semicinctus*, *T. wrighti*, and *T. feicki*. Both Jamaica and Hispaniola have representatives of *T. haetianus*, and the Bahamas are occupied by *T. canus*, with *T. greenwayi* on the outlying Caicos Bank. The genus is absent from Puerto Rico and the Lesser Antilles; it does occur in South America (*T. paucisquamis*, *T. taczanowskyi*), on the Cayman Islands (*T. melanurus caymanensis*, *T. melanurus parkeri*), and Navassa Island (*T. bucculentus*).

We have examined one specimen of *taczanowskyi* and one of *T. paucisquamis*. Stull (*op. cit.*:4) postulated origin of the West Indian forms from both of these South American snakes; she had not examined hemipenes of either of them. The single

T. taczanowskyi (USNM 119009) is a female; the *T. paucisquamis* (AMNH 72426) is a new-born male and apparently has bifurcate hemipenes. Of the two, *paucisquamis* has 21 scale rows and smooth dorsals, whereas *taczanowskyi* has 23 scale rows and prominently keeled dorsals — in fact, far more prominently keeled than those of any of the *pardalis-maculatus* group from the West Indies. Judging from Stull's descriptions and our examination, both of these species seem closer to the assemblage of forms under discussion than they do to either the *melanurus-bucculentus* group or the *semicinctus* group. Of the two, *taczanowskyi* appears more closely related, and *paucisquamis* more distantly related, to the assemblage. The dorsum of *taczanowskyi* is pale tan with three faintly indicated rows of blotches. The ventral blotches are large and black, and very prominent. These blotches are quite comparable to the ventral blotches of *T. pardalis.* The low ventral count (150), pale tail, and 23 scale rows all seem to ally *taczanowskyi*, in addition, to *pardalis.* However, the very distinctly keeled scales and the much faded dorsal pattern (with apparently three faint rows of blotches dorsally) serve to distinguish the two forms at once.

The single *T. paucisquamis* is so small that little can be determined about it. The blotches are apparently in eight longitudinal rows, and the entire tail is pale yellow dorsally and has four bold black blotches ventrally; this scheme of coloration and pattern is like that of none of the West Indian snakes. The venter has two longitudinal rows of irregular black blotches, reminiscent of, but not exactly like, those of *pardalis.* The dorsal pattern is peculiar, having a distinctly pale middorsal band about six scales in width, its margins scalloped by the lateral dusky ground color and the paramedian blotch rows. All these factors, plus the low number of scale rows (21), seem to set off *T. paucisquamis* from consideration as being on any direct line of origin for any of the West Indian forms; its very different characteristics indicate that it and the West Indian snakes have had a long and isolated history. Certainly additional specimens of both *T. tacznawoskyi* and *T. paucisquamis* are badly needed for study.

If we assume that there has been an increase in number of scale rows within the genus, then, of the *pardalis-maculatus* complex, those species with the lower number of dorsal scale rows (*pardalis*, *canus*, and *nigriventris*) will be the more primitive, and that with the higher number of scale rows (*haetianus*) will be the more advanced, with the remaining species between. The nature of the carination of the dorsal scales may not be profitably used since in all taxa of the group both keeled and unkeeled snakes occur; we think however that carinate dorsals are more primitive than smooth dorsals.

It is interesting to note that of the three species just mentioned as having a low number of scale rows, two (*pardalis, nigriventris*) occur on Cuba (Fig. 10), and the third (*canus*) may possibly be there. The close affinities of *nigriventris* and *pardalis* have already been commented upon. *T. canus* and its subspecies in the Bahamas may well have been derived from *pardalis* in eastern Cuba (where it may occur still), or the occurrence of *T. canus* in eastern Cuba may represent a re-invasion into that area from the Bahamas. The latter is not likely however, since the currents along the north coast of Cuba flow towards, rather than from, the Bahamas (Marrero, 1951:44). It is interesting to note also that *T. c. canus* almost regularly (19 of 20 specimens) has 23 scale rows; this subspecies occurs on Great Inagua Island, that Bahaman island closest to the Cuban mainland, with the exception of the Cay Sal Bank group of keys. Differentiation on the Bahamas has been relatively slight, involving differences in number of ventrals, keeling of dorsals, obsolescence of juvenile pattern, and size; *T. greenwayi* stands as a notable exception to this statement. This species may well be a *T. canus* derivative, isolated, as far as known, on the rather remote Caicos Bank, which is separated from the Inaguas to the southwest and from the Acklin-Crooked island mass by deep troughs. No *Tropidophis* are known from either the islands of the Little Bahama Bank to the north, or from the more eastern islands (Rum Cay, San Salvador, Crooked, Acklin, Mayaguana, or Little Inagua) with the exception of the islands and cays of the Caicos Bank, where *T. greenwayi* is presumed to occur. The extreme differences of this species bespeak a long isolation from the remainder of the members of the group.

T. maculatus, *T. nigriventris*, and *T. pilsbryi* have the basic distribution characteristics of other Cuban amphibians and reptiles which have had rather long independent histories due to isolation on islands when Cuba was either an archipelago or several isolated islands corresponding roughly to the modern mountain masses. Thus, *T. maculatus* probably arose from a *T. haetianus*-like ancestor in the area of the Sierra del Rosario-Sierra de los Organos, *T. nigriventris* in the Sierra de Trinidad, and *T. pilsbryi* in the Sierra Maestra. Each of these is more or less still restricted to these areas, although *nigriventris* has apparently spread to the east into Camagüey, and *pilsbryi* has spread to the west into Las Villas.

T. haetianus with 25 and 27 (and occasionally 29) scale rows seems to be the most advanced member of the complex; on Jamaica it has differentiated into three forms, whereas on the much larger island of Hispaniola only one form is known. This may indicate either a much longer residence on Jamaica than on Hispaniola, or that the species has been overly "split" taxonomically on the former island and that several subspecies occur on Hispaniola which are at present not or poorly represented in Hispaniolan material. As far as we are concerned, Hispaniolan material shows no striking differences within itself; this is rather surprising considering the subspecific differentiation of such snake genera as *Leimadophis* on Hispaniola. We postulate that *T. haetianus* is a relatively recent arrival to Hispaniola. Its occurrence in eastern Cuba is somewhat puzzling, but the similarity of Cuban and Hispanolian material may well indicate that this species has arrived at both islands from Jamaica at about the same time, and that little subsequent differentiation has taken place. Of the three Jamaican subspecies, we feel that *haetianus* and the Cuban snakes can best be derived from the more generally patterned, usually smooth scaled *jamaicensis*, which has an intermediate number of ventrals.

Darlington (1957:510 *et seq.*) discussed at some length the zoogeography of the West Indies. He postulated a double origin of the West Indian fauna, partially derived through migration via Cuba, and partially via Jamaica. Both invasions were presumably from Central America. If such a double origin is true, and there is no reason for doubting it, then the species of *Tropidophis* may be categorized in the following way. We imagine that *pardalis* is the basic stock in Cuba from which were derived *nigriventris* by isolation in the old Sierra de Trinidad, and *T. canus* via invasion of the Bahamas from Cuba. Of these two derived forms, the separation of *canus* and *pardalis* has been the longer. The relationships of *T. greenwayi* remain uncertain: it may either represent a long isolated offshoot of *T. canus*, or of *T. pardalis*, or it may have had some completely unknown history. The basic continental stock for this group of forms is most likely *T. taczanowskyi*, for reasons mentioned above. In the series, the number of scale rows goes from the primitive condition of 23 rows (*taczanowskyi*, *pardalis*, *nigriventris*, *canus*, *curtus*) to 25 (*androsi*, *barbouri*, and *greenwayi*).

Invasion of the West Indies via Jamaica can be used to account for the distributional pattern of *T. haetianus,* with forms on Jamaica, Hispaniola, and Cuba. We suspect that *pilsbryi* and *maculatus* represent isolates from this basic stock, isolates which have had long independent histories in the Sierra Maestra and the Sierra de los Organos respectively. In this second group of species, the scale rows are 25 in the more primitive members (*stulli, maculatus, pilsbryi* (?), and Cuban *haetianus*) to 27 (occasionally 29) in the more advanced members (*jamaicensis, haetianus, stejnegeri*).

Specimens examined

Tropidophis canus androsi: *Bahamas:* Andros Island, 8 (AMNH 2925-27, 63112; USNM 49471-72, 49474, 64156); Mangrove Cay, Andros Island, 2 (AMNH 63113; UMMZ 103982).

T. canus barbouri. Bahamas: Long Island, Clarencetown, 6 (AMNH 77008-12; UMMZ 117024); Long Island, Simm's, 1 (UMRC 55.139); Warderick Wells Cay, Exuma Cays, 1 (AMNH 77013); South Eleuthera Island, 2 (USNM 120804-05); Eleuthera Island, 3 (AMNH 73836-37; UMMZ 117278); Eleuthera Island, Hatchet Bay, 2 (AMNH 69178; UMMZ 99227).

T. canus canus. Bahamas: Great Inagua Island, 3 (AMNH 63335-37); Great Inagua Island, southwest point, 10 (AMNH 45839-47; UMMZ 117025); Matthew Town, Great Inagua Island, 1 (AMNH 45838); Inagua Island, 6 (USNM 26736, 7111 (5 specimens)).

T. canus curtus. Bahamas: New Providence, 19 (USNM 36594-95; MCZ 6241, 6491, 6969 (4 specimens), 6780, 6781 (2 specimens), 7089, 7090 (3 specimens); ANSP 10271-74); Nassau, New Providence, 7 (AMNH 2617, 7713; MCZ 8734-38); "British West Indies," 1 (ANSP 10278); no data, 3 (ANSP 10282-84); Bimini, 6 (AMNH 73501-04; UMMZ 110869-70); South Bimini, 8 (AMNH 73542, 73708, 75414-18, 75623); South Bimini, north side, 2 (AMNH 76870-71); South Bimini, west end, 1 (AMNH 68818).

T. canus subsp. *Bahamas:* Cay Sal Bank, Doubleheaded Shot Cay, 1 (USNM 81536); *Cuba,* Camagüey Prov., Nuevitas, 1 (AMNH 2946).

T. greenwayi. Bahamas: Ambergris Cay, Caicos Island, 2 (MCZ 42051-52).

T. maculatus. Cuba, Pinar del Río Prov., Guane, 1 (MCZ 10836); Pinar del Río, 1 (MP); Viñales, 1 (MP 179); Puerta del Ancón, 1 (MP); Consolación del Sur, 1 (MP); La Deseade, 1 (MP); Habana Prov., Almendares, 1 (MP 186); La Habana, 3 (MP, MCZ 22901, USNM 56328); La Habana?, 1 (MP 59); Botanical Gardens, La Habana, 2 (MCZ 7930-31); Bosque de la Habana, La Habana, 1 (MP 286); near Río Quibús, Marianao, 1 (MBZH 26); Managua, 2 (MP 23); no locality other than Cuba, 1 (ANSP 10250); *Isla de Pinos*, no other locality, 1 (MCZ 12445).

T. pilsbryi. *Cuba*, Las Villas Prov., Mina Carlota, 1 (UMMZ 65043); Oriente, Cayo del Rey, near Miranda, 1 (ANSP 20822); Guantánamo, 1 (MCZ 9884); "eastern Cuba," 1 (USNM 12361).

T. pardalis. *Cuba*, Pinar del Río Prov., Pedrera de Mendoza, Mendoza, Guane, 1 (MBZH 62); 2 kilometers from Artemisa, 1 (MBZH 17); El Guamá, 1 (USNM 27392); San Diego de los Baños, 1 (USNM 27849); La Deseade, 2 (MP); Herradura, 1 (MP 183); Habana Prov., Bosque de la Habana, La Labana, 8 (MBZH 59, 66; MP (6 specimens)); Cojímar, 1 (MBZH 19); El Cotorro, 7 (AMNH 76541-47); La Habana, 3 (USNM 58715-17); 9 kilometers southeast of San José de las Lajas, 2 (AMNH 77783, 76563); La Ceiba, Marianao, 2 (MP); Marianao, 1 (MP 111); Country Club, Marianao, 1 (MP); Rio Quibús, Marianao, 1 (MP); Jaruco, 1 (MP); Escaleras de Jaruco, 1 (MP 299); Baracoa, 1 (MP 306); Caimito, 2 (MP); Ceiba del Agua, 1 (MP); Matanzas Prov., Matanzas, 2 (MP 546; USNM 26360); Abra de Yumurí, 1 (MP 319); Las Villas Prov., Soledad, 3 (AMNH 77784; USNM 134355; UMMZ 76109); La Sierra, north of Vega Alta, 1 (USNM 75823); Cumanayagua, 1 (MP); Trinidad, 2 (USNM 137085, 138511); Camagüey Prov., Paredón Grande, 1 (MBZH); Oriente Prov., San Germán, 5 (MP 200 (3 specimens), 213 (2 specimens)); Cuba, no other locality, 10 (USNM 12418, 36804; UMRC 55.503; ANSP 10251-56, 10280); *Isla de Pinos*, no other locality, 8 (CM 1522-23, 1526, 1528-31, 284; east base, Sierra de las Casas, just west of Nueva Gerona, 2 (AMNH 78605, 81000).

T. nigriventris. *Cuba:* Las Villas Prov., Trinidad, 1 (USNM 138512); 10 miles west of Trinidad, 1 (USNM 138510); Camagüey Prov., Martí, 1 (UMMZ 70887); Finca El Porvenir, Loma de la Yagua, 24 kilometers southwest of Camagüey, 2 (AMNH 81182-83).

T. haetianus haetianus. *Haiti:* Port-au Prince, 1 (USNM 70459); Trou Forban, 1 (USNM 117279); *Republica Dominicana*, Puerto Plata, 1 (USNM 10275); San Francisco Mountains, 1 (USNM 35979); nr. Cape Samaná, 1 (USNM 55046);

Guarabo, 1 (USNM 66716); Paradis, 2 (USNM 64910); "eastern Santo Domingo," 1 (ANSP 10279); "Santo Domingo?", 2 (USNM 14838 (2 specimens)); Gonave Island, En Cafe, 1 (USNM 75925).

T. haetianus jamaicensis. Jamaica: Kingston, 1 (MCZ 44871-72); Long Mt., Kingston side, 1 (MCZ 59202); Malvern, 4 (MCZ 59203, 59205, 59207-08); Malvern, Santa Cruz Mountains, 1 (MCZ 55745); Mona, 3 (MCZ 59204, 59206, plus one untagged); "West Indies," no other locality, 1 (MCZ 6707).

T. haetianus stulli. Jamaica: Portland Point, 2 (MCZ 44871-72).

T. haetianus stejnegeri. Jamaica: Montego Bay, 3 (USNM 42878-80); Balaclava, 1 (USNM 73275).

T. haetianus subsp. *Cuba:* Las Villas Prov., Soledad, Cienfuegos, 1 (USNM 137084); Oriente Prov., Guardalavaca, Banes, 1 (MCZ 47896); "eastern Cuba," 1 (USNM 27455).

T. taczanowskyi. Peru: Loreto Prov., Fundo Sinchono, 1 (USNM 119009).

T. paucisquamis. Brazil: Boracea, São Paulo, 1 (AMNH 72426).

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TABLE 1

Data on sixteen populations of *Tropidophis* from the West Indies.

Form	N		Largest specimen (total length)		Longest tail	
	♂	♀	♂	♀	♂	♀
pardalis (Cuba)	23	24	343	292	44	45
pardalis (Isla de Pinos)	6	4	315	284	51	35
nigriventris	2	3	351	355	48	31
maculatus	8	9	375	394	48	47
pilsbryi	2	2	212	—	31	—
jamaicensis	3	7	383	340	45	38

Table I (Continued)

Form	N		Largest specimen (total length)		Longest tail	
	♂	♀	♂	♀	♂	♀
stulli	2	0	318	—	35	—
stejnegeri	1	3	416	362	50	39
haetianus (Hispaniola)	3	8	400	712	56	76
haetianus (Cuba)	1	2	212	244	28	24
canus	8	12	408	373	45	40
curtus (New Providence)	12	18	330	310	47	39
curtus (Bimini)	6	11	359	362	49	52
androsi	7	3	320	317	47	37
barbouri	9	6	365	334	50	38
greenwayi	2	0	355	—	42	—

TABLE II

Data on sixteen populations of *Tropidophis* from the West Indies.

Form	T/T1 X100 (mean and extremes)	Tail color (adults)	
		dark	light
pardalis (Cuba)	12.9 (10.5-16.5)	2	45
pardalis (Isla de Pinos)	13.6 (11.9-16.1)	0	7
nigriventris	13.1 (13.0-13.2)	1	1
maculatus	12.2 (11.1-13.3)	4	10
pilsbryi	12.3 (11.0-14.6)	1	1
jamaicensis	11.0 (10.0-12.9)	4	5
stulli	11.6 (11.0-12.2)	0	2
stejnegeri	11.5 (10.8-12.0)	1	2
haetianus (Hispaniola)	13.3 (12.3-15.1)	6	2
haetianus (Cuba)	13.1 (13.0-13.2)	2	1
canus	10.7 (9.4-12.1)	14	5
curtus (New Providence)	13.5 (12.1-15.2)	26	2
curtus (Bimini)	13.7 (11.6-14.9)	4	2
androsi	13.0 (11.6-14.7)	8	1
barbouri	12.6 (11.0-14.4)	7	4
greenwayi	11.9	0	2

TABLE III
Data on sixteen populations of *Tropidophis* from the West Indies.

Form	Rows of blotches (incidence in ( ))	Dorsal spots	Occipital spots (adults) present	absent
pardalis (Cuba)	6(51); 8(4)	25-42	18	30
pardalis (Isla de Pinos)	6(4); 8(5)	31-41	8	0
nigriventris	8(5)	37-46	0	5
maculatus	6(1); 8(14); 10(1)	33-54	0	14
pilsbryi	8(3); 10(1)	38-50	2	0
jamaicensis	8(2); 10(6)	45-54	0	9
stulli	10(2)	44-50	0	2
stejnegeri	8(2); 10(1)	49-56	3	0
haetianus (Hispaniola)	8(5); 10(6)	45-57	0	11
haetianus (Cuba)	10(3)	45-51	1	2
canus	6(10); 7(1); 8(7); 9(1)	40-59	0	19
curtus (New Providence)	8(2); 10(22)	40-56	0	28
curtus (Bimini)	8(1); 9(2); 10(9); 11(2); 12(3)	40-90	0	8
androsi	10(9)	43-53	0	9
barbouri	8(5); 9(2); 10(6)	38-53	0	12
greenwayi	8(1); 10(1)	39-44	0	2

TABLE IV
Data on sixteen populations of *Tropidophis* from the West Indies.

Form	Parietal contact present	absent	Dorsal scales keeled	smooth
pardalis (Cuba)	15	42	2	50
pardalis (Isla de Pinos)	6	4	0	10
nigriventris	0	5	0	5
maculatus	6	10	11	8
pilsbryi	0	4	3	1
jamaicensis	2	8	0	10
stulli	0	2	0	2
stejnegeri	0	4	4	0
haetianus (Hispaniola)	10	1	1	10
haetianus (Cuba)	1	2	2	1
canus	6	14	12	2
curtus (New Providence)	4	26	27	3
curtus (Bimini)	2	15	5	12
androsi	0	9	8	0
barbouri	0	15	12	2
greenwayi	2	0	0	2

TABLE V

Data on sixteen populations of *Tropidophis* from the West Indies.

	Postoculars				Scale rows			
Form	$^2_2$	$^2_3$	$^3_3$	other	23	25	27	other
pardalis (Cuba)	42	7	8		39	14	0	21(1); 22(2); 24(2)
pardalis (Isla de Pinos)	4	1	5		6	4	0	
nigriventris	3	0	2		3	1	0	24(1)
maculatus	1	1	15		0	16	0	
pilsbryi	0	0	4		1	1	1	
jamaicensis	1	0	6		0	4	3	26(1); 29(1)
stulli	0	0	2		0	2	0	
stejnegeri	1	0	2		0	1	3	
haetianus (Hispaniola)	0	0	9	3/5 (1)	0	0	11	
haetianus (Cuba)	0	0	3		0	2	0	26(1)
canus	2	1	17		19	0	0	22(1)
curtus (New Providence)	14	6	10		17	12	0	24(1)
curtus (Bimini)	3	2	9	3/4 (1)	4	9	0	24(4)
androsi	3	0	7		1	7	0	24(2)
barbouri	2	6	7		6	8	0	24(1)
greenwayi	2	0	0		0	2	0	

TABLE VI

Data on sixteen populations of *Tropidophis* from the West Indies.

Form	Ventrals	Caudals
pardalis (Cuba)	147.1 (140-165)	28.2 (23-34)
pardalis (Isla de Pinos)	149.5 (147-155)	29.9 (28-32)
nigriventris	155.0 (144-170)	25.5 (25-26)*
maculatus	197.6 (189-208)	36.3 (24-41)
pilsbryi	167.0 (160-178)	30.5 (30-31)
jamaicensis	174.3 (169-178)	32.8 (30-36)
stulli	166.5 (166-167)	33.0 (32-34)
stejnegeri	186.0 (184-187)	32.3 (31-33)
haetianus (Hispaniola)	185.2 (180-192)	37.0 (33-39)
haetianus (Cuba)	184.0 (178-191)	33.5 (33-34)
canus	174.7 (178-191)	30.8 (29-35)
curtus (New Providence)	151.8 (149-157)	32.2 (29-37)
curtus (Bimini)	153.8 (146-160)	31.2 (29-36)
androsi	164.0 (157-173)	32.4 (30-36)
barbouri	158.3 (154-165)	29.9 (22-33)
greenwayi	157.5 (157-158)	30

*33 in male with incomplete tail.

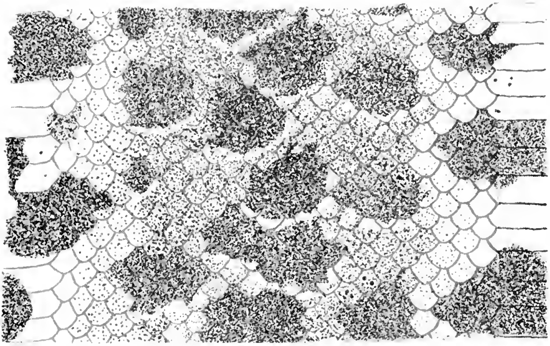

Fig. 1. *Tropidophis pardalis*, pattern at midbody; AMNH 77784, from Soledad, Las Villas Province, Cuba.

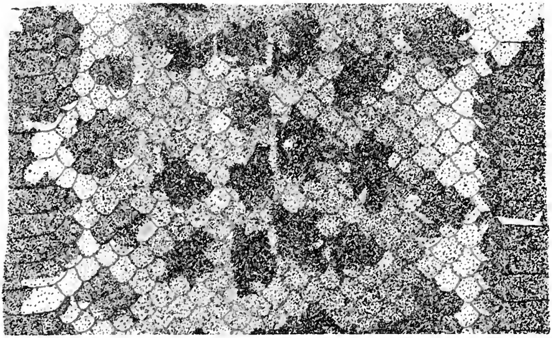

Fig. 2. *Tropidophis nigriventris*, pattern at midbody; UMMZ 70887, paratype, Martí, Camagüey Province, Cuba.

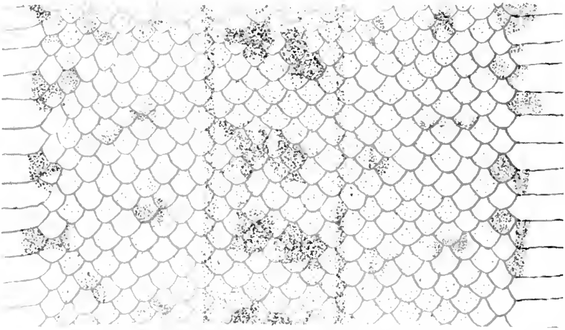

Fig. 3. *Tropidophis haetianus stulli*, pattern at midbody; MCZ 44871, paratype, Portland Point, Jamaica.

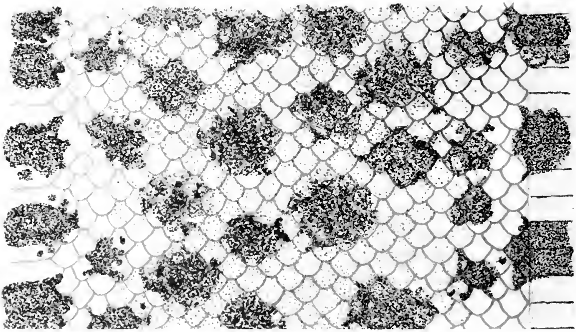

Fig. 4. *Tropidophis maculatus*, pattern at midbody; USNM 56328, from La Habana, Habana Province, Cuba.

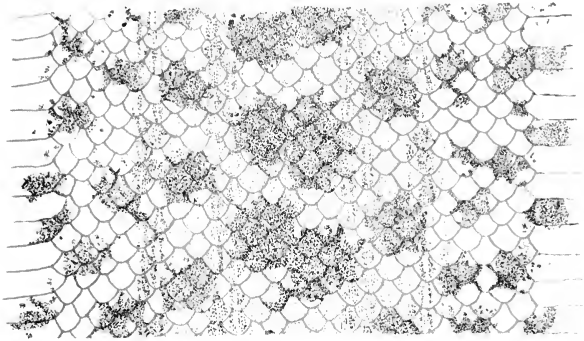

Fig. 5. *Tropidophis canus barbouri*, juvenile, pattern at midbody; AMNH 77008, from Clarencetown, Long Island, Bahamas, B.W.I.

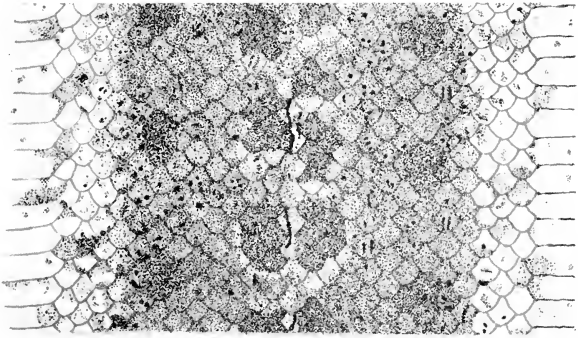

Fig. 6. *Tropidophis canus barbouri*, adult, pattern at midbody; AMNH 77010, from Clarencetown, Long Island, Bahamas, B.W.I.

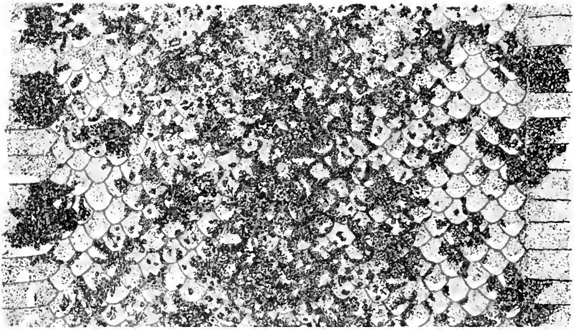

Fig. 7. *Tropidophis greenwayi*, pattern at midbody; MCZ 42051, type, Ambergris Cay, Caicos Island, Bahamas, B.W.I.

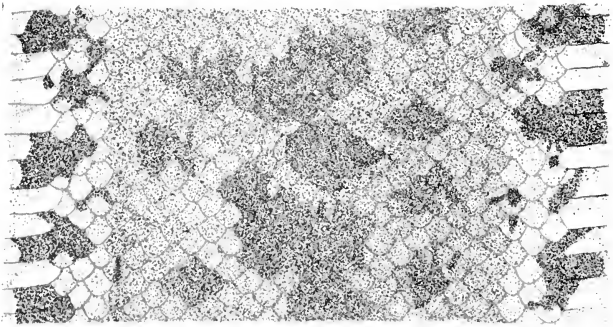

Fig. 8. *Tropidophis haetianus haetianus*, pattern at midbody; USNM 70459, from Port-au-Prince, Haiti, Hispaniola.

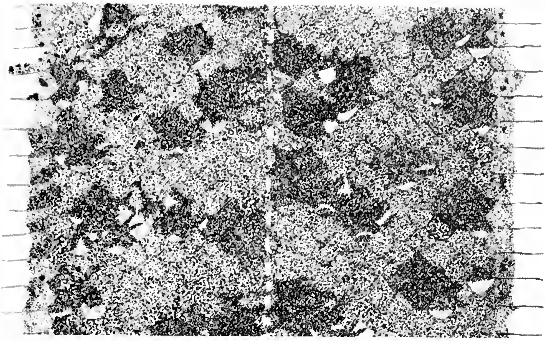

Fig. 9. *Tropidophis pilsbryi*, pattern at midbody; MCZ 9884, paratype, Guantánamo, Oriente Province, Cuba.

Fig. 10. Map of the Bahamas, Cuba, Isla de Pinos, Hispaniola, and Jamaica, showing the distribution of the species recognized in the present paper. Symbols are as follows: *T. canus*, stippling; *T. haetianus*, broad vertical bars; *T. maculatus*, narrow vertical bars; *T. pardalis*, diagonal bars; *T. pilsbryi*, horizontal bars; *T. greenwayi*, arrow; *T. nigriventris*, area in Cuba enclosed by dashed line. The extension of both *T. canus* and *T. haetianus* to Cuba is based on specimens as noted in text.

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AT HARVARD COLLEGE
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EIGHT HISTORIC FOSSIL MAMMAL SPECIMENS IN THE MUSEUM OF COMPARATIVE ZOOLOGY

By Horace E. Wood, 2nd
Emeritus Professor, Rutgers University
and
Research Associate in Fossil Mammals,
American Museum of Natural History

WITH ONE PLATE

PRINTED FOR THE MUSEUM
CAMBRIDGE, MASS., U.S.A.
September, 1960

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INTRODUCTION

For a quarter of a century I have planned to restudy several neglected and inadequately known fossil mammals in the Museum of Comparative Zoology. These specimens, seven rhinoceroses and an entelodont, include the types from the "auriferous gravels" of California that Leidy described in 1865 and 1869 and that Whitney carried to Harvard following his colorful controversy at the California Academy of Natural Sciences. Scott and Osborn's types (1887) collected in the Big Badlands in 1880-81 by Samuel Garman are reassigned; and for the first time an illustration of the dentition of the type of *Metamynodon planifrons* appears in print. In general, this study simplifies rhinoceros taxonomy. The unusual historic associations and stratigraphic significance of these half-forgotten genera should revive interest in this small collection.

My thanks go to Dr. A. S. Romer for permission to redescribe this interesting assemblage and to his staff for their assistance. The collections at the American Museum of Natural History and Yale Peabody Museum have also afforded valuable comparative material. Some unpublished drawings by the late Rudolph Weber are included, and, as always, I am deeply grateful to Florence D. Wood, who provided the remaining illustrations. Grants from the Rutgers University Research Council assisted this investigation.

Specimen numbers carry abbreviations indicating the institutions which house them. A.M.N.H. refers to the American Museum of Natural History; C.I.T. refers to California Institute of Technology. In this connection, the Los Angeles County Museum, Los Angeles, California, now contains the entire former paleontological collection from California Institute of Technology. M.C.Z. is Museum of Comparative Zoology; P.U. is Princeton University; and Y.P.M. is Yale Peabody Museum.

SYSTEMATIC DESCRIPTIONS

Order ARTIODACTYLA

Family ENTELODONTIDAE

ARCHAEOTHERIUM SUPERBUM (Leidy), 1868

Figure 1 *A-C*

Elotherium superbus Leidy, 1868, p. 177.
Elotherium superbum, Leidy, 1869, p. 388.
Archaeotherium superbum, Troxell, 1920, p. 244.
Entelodon superbum, Allen, 1931, p. 281.

Type. M.C.Z. No. 9564, right I^3, the only known specimen (Fig. 1, *A-C*).

Horizon and locality. Deep "auriferous gravels," Oligocene, probably middle, Douglas (or Douglass) Flat, Calaveras County, California.

Diagnosis. Referable to the genus *Archaeotherium*, larger than *A. mortoni*, close to *A. wanlessi*, smaller and more primitive than the largest giant pigs, such as *Megachoerus*, *Daeodon* and *Dinohyus*.

This specimen, out of place among rhinoceroses, is discussed here in order to treat the Whitney collection as a unit. Apparently collected in 1867, and now figured for the first time, the tooth was tentatively identified as a hyaena canine by Whitney (1867 b). Leidy (1868) gave an accurate verbal description, correctly referring it to *Elotherium,* which was republished in essentials by him (1869, p. 388) and by Whitney (1879, pp. 244-245, 283). Subsequent workers evidently found this description useless without the specimen or illustration. Peterson (1909, p. 69) considered that "this species should be regarded as only possessing value from the standpoint of history and geographic distribution," i.e., in modern terminology, he considered it a *nomen dubium.* This opinion was apparently endorsed by Troxell (1920, p. 250), and the issue was not reopened by Sinclair (1922 a and b), by Allen (1931, p. 281) who listed this specimen among M.C.Z. types, or by Scott (1940).

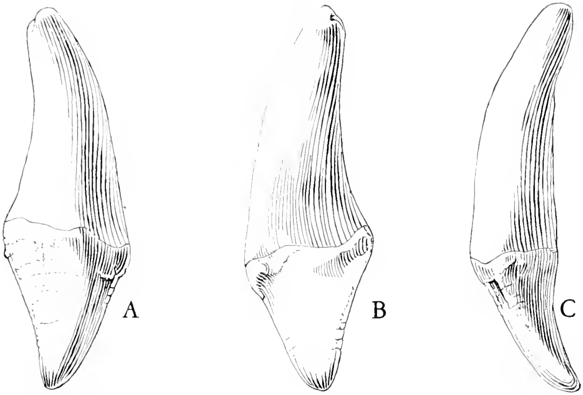

Fig. 1. *Archaeotherium superbum,* type, M.C.Z. No. 9564, right I^3, x 1. *A,* buccal aspect; *B,* lingual aspect; *C,* medial aspect.

It was also my first impression that this species could best be treated as a *nomen dubium,* but, inadequate as the type specimen is, detailed comparisons show that it can yield considerable information. Leidy's tentative identification as the right upper lateral incisor is fully confirmed, as is Troxell's reference to the genus *Archaeotherium.* I follow Peterson (1909), Troxell (1920), Sinclair (1922a), and Scott (1940) in separating *Archaeotherium* Leidy generically from the European form, whether one prefers to call the latter *Entelodon* or *Elotherium.* As

Leidy stated, it is larger than *A. mortoni*. It is neither *Dinohyus* nor any of the large Whitneyan forms. It is far smaller than *?Megachoerus praecursor* Scott, type A.M.N.H. No. 572, from the upper Oreodon beds (Scott, 1940, pp. 426, 435-436 and 736). Although it does not exactly duplicate any American Museum specimen, it compares best with middle-sized Chadronian and Orellan specimens. Despite the work of Peterson, Troxell, Sinclair and Scott, the taxonomy of the middle-sized archaeotheres (i.e., the next larger size grade than *A. mortoni*) is in a sadly muddled state. Without trying to decide what specific name or names may be valid, I find the closest match to this tooth in the type of *Archaeotherium wanlessi* Sinclair, P.U. No. 12552 (Scott, 1940, Pl. 40, fig. 1) from the turtle-oreodon zone of the Scenic Member (Bump, 1956) of the Brule formation. The stratigraphic significance of this specimen is discussed below, in connection with *Subhyracodon occidentalis*, M.C.Z. No. 9119. There is an excellent cast of *Archaeotherium superbum* in the American Museum, A.M.N.H. No. 9975.

Order PERISSODACTYLA

Family RHINOCEROTIDAE

Subhyracodon hesperius (Leidy), 1865

Figure 2 *A*, *B*

Rhinoceros hesperius Leidy, 1865, p. 176.

Aphelops hesperius, Roger, 1887, p. 56.

Aceratherium hesperium, Osborn, 1898, pp. 144-145.

Aceratherium (Aphelops) hesperium, Trouessart, 1898, pp. 747-751.

Diceratherium hesperium, Hay, 1902, p. 644.

Type. M.C.Z. No. 9118, a symphysis and right ramus, with I_2 left, M_{1-3} right, and the roots or alveoli of the intervening teeth (Fig. 2, *A*, *B*, and Leidy, 1869, Pl. 23, figs. 11 12), and a separate portion of the left condylar region, supposed to be associated, probably correctly.

Horizon and locality. Mid-Tertiary "auriferous gravels" channel, probably Oligocene, Chili Gulch, Calaveras Co., California.

Diagnosis. Lower jaw of *Subhyracodon* character, about the size and shape of *S. tridactylus*, I_2 C_0 P_4 M_3; premolar series relatively short, molars closest to *S. occidentalis* in size and character but with weaker external and internal cingula; molars noticeably smaller and slighter than in *S. tridactylus*.

Whitney (1865, pp. 251 and 268) announced the former occurrence of the rhinoceros in California on the basis of this specimen. Leidy (1865) described and named it; later (1869, pp. 230-231, 390, Pl. 23, figs. 11-12), he redescribed it in more detail, in his usual, extraordinarily able fashion, and with his usual exact illustrations. His Plate 23, figure 11, shows the left I_2 reversed, as a right I_2, in external aspect. After the abrupt discontinuance of the California Geological Survey, Whitney took this specimen, as well as the other fossil vertebrates, including the controversial Calaveras human skull, to Harvard. He redescribed M.C.Z. No. 9118 (1879, pp. 243-244, 283), largely by quoting from Leidy. Thereafter, the location of this collection seems to have dropped out of general knowledge. Osborn (1898, p. 144) supposed it to be in California; Peterson (1920, p. 411) called the "location of the type uncertain," apparently with some additional confusion as to what the type specimen was. Troxell (1921, p. 197) merely called the type "inadequate," without further discussion. Allen (1931, p. 287) listed it among M.C.Z. types. Stock (1933, pp. 22-23) discussed this specimen in connection with his description of *Subhyracodon kewi*, also mentioning its presence in the M.C.Z. collections. There is a satisfactory cast of this jaw in the American Museum, A.M.N.H. No. 9973.

The jaw, which is undistorted, compares closely in total length, in length of symphysis, and in depth, with *Subhyracodon tridactylus* (e.g., A.M.N.H. No. 538, the type, and A.M.N.H. Nos. 534 and 1126). The separate left condylar region, also of a rhinoceros of *Subhyracodon* aspect, resembles *S. tridactylus* generally, but has a more rugose postcotyloid process. The lower profile of the chin and horizontal ramus are characteristic of *Subhyracodon* in general and of *S. tridactylus* in particular. The jaw, by itself, could be assigned to *S. tridactylus*, but it is well outside the known geographic range of *S. occidentalis*, including its advanced variant, *S. metalophus*. On the other hand, as Leidy recognized, the teeth (Fig. 2, *A*, *B*, and Leidy, 1869, Pl. 23, fig. 12) are closest to *S. occidentalis* among Great Plains forms. The alveoli of I_1, right and left, are of good size, about as in *S. occidentalis*. Right I_2 is broken off at the root and left I_2, though well worn, is long. This lower tusk varies extensively with wear, and, perhaps, sex: that of M.C.Z. No. 9118 is rather large and long for *S. occidentalis* but is exceeded in cross-section and, probably, in original length, by I_2 of A.M.N.H. No. 38995, an unusually large individual. This tusk is well worn in M.C.Z. No. 9118, ovoid in cross-section, tapering somewhat medially, with indications that a small median flange may have formerly been present, but worn off. There is no trace of I_3 or C_1 and the diastema, like the symphysis, is rather long for the size of the jaw. The premolars are broken off at the gum line. P_1 (or dP_1) had a single small root; P_{2-4} were two rooted, increasing in size, caudally. Relative to the length of the jaw and the size of the molars, the premolars are small in both dimensions, even allowing for the exaggeration of this impression by their being broken off at the gum line. This raises the question as to whether the premolars were primitively small or secondarily reduced. The characters of the teeth and jaw make the second alternative seem much more probable. The molars are moderately worn; the anterior third of M_1 is broken off; M_2 is substantially intact; much of the talonid of M_3 is missing. As Leidy indicated, the molar patterns are close to *S. occidentalis*, with perfectly simple crescents. However, the California specimen has much weaker cingula. The anterior cingula of M_{2-3} are moderately strong, but more like *Caenopus* than *Subhyracodon:* the posterior cingula of M_{1-2} are obscure, but also seem weak

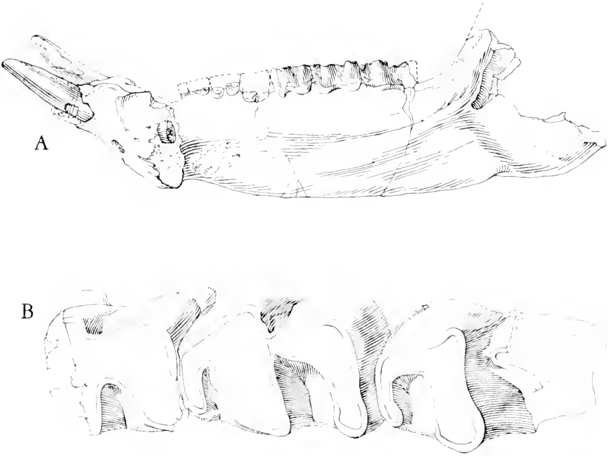

Fig. 2. *Subhyracodon hesperius*, type, M.C.Z. No. 9118. *A*, symphysis and lingual aspect of right ramus, right I_2 reversed from left I_2, x .23; *B*, right M_{1-3}, crown view, x .798.

compared with *Subhyracodon.* Internal cingula are altogether absent on M_1 and from the preserved portions of M_2 and M_3. M_1 has a very weak but continuous external cingulum, which is represented on M_{2-3} only by a trace across the median valleys.

Varied relationships have been suggested for this form. Leidy correctly indicated both its resemblances to and its differences from *S. occidentalis*, regarding them as related species. On the other hand, Osborn considered it close to *Amphicaenopus platycephalus* Roger, and Trouessart assigned it to *Aphelops* for reasons which are purely speculative. Hay assigned it to *Diceratherium,* in which he was followed by Loomis (1908, p. 55), Peterson (1920, p. 411) and, more positively, by Troxell (1921b). Stock (1933, pp. 22-23) suggested that M.C.Z. No. 9118 might as well be a large *Subhyracodon* as a *Diceratherium;* he considered the possibility that his new species, *Subhyracodon kewi,* might be conspecific with M.C.Z. No. 9118, and decided against it, an opinion with which I fully concur. It seems unnecessary to prove that the specimen is not generically referable to *Rhinoceros, Aceratherium* or *Aphelops.* There is no significant resemblance to American Museum specimens of *Amphicaenopus platycephalus* whether from the lower or upper Oligocene. It is certainly not *Trigonias, Caenopus, sensu stricto,* nor *Diceratherium cooki.* Significant resemblances are limited to the *Subhyracodon-Diceratherium* lineage; and inside this lineage, to *S. occidentalis, S. tridactylus* and *Diceratherium.* This specimen does not match any in the American Museum's large collection of *S. occidentalis;* its size exceeds even the biggest, A.M.N.H. No. 38995. Among specimens of *S. occidentalis,* the molars are closest to A.M.N.H. No. 39110. However, the premolars of M.C.Z. No. 9118 are markedly smaller, and the series as a whole shorter, although the teeth of A.M.N.H. No. 39110 were considerably more shortened by interstitial wear. Comparison with *S. metalophus,* an advanced variant of *S. occidentalis,* represented by the type, Y.P.M. No. 10254, and by A.M.N.H. No. 1123, also fails for much the same reasons but to a slightly lesser degree. Although the jaw of *S. hesperius* roughly agrees with *S. tridactylus* the molars are too small and delicate for such an assignment. (If they were conspecific, *S. hesperius* would have twenty-eight years' priority over *S. tridactylus.*) Comparison with the John Day diceratheres at Yale and the American Museum also fails to disclose any very close match. M.C.Z. No. 9118 is larger than *Diceratherium annectens* and smaller than *D. armatum,* without any striking resemblance in detail to either. Taking all these resemblances and differences into account, I conclude that M.C.Z. No. 9118 represents a valid species, that no other known material agrees sufficiently closely with it to be conspecific, that it must be assigned to the genus *Subhyracodon*, and that its age may be tentatively considered as late Oligocene.

Whitney (1865, p. 268, and 1879, pp. 128-129, 243) briefly described the geology of Chili Gulch, from which this is the only known vertebrate. The range in probable age appears to be from Orellan to Whitneyan; Whitneyan is more likely because of the larger size and reduced premolars, compared with *S. occidentalis*. This species represents a separate evolutionary trend from *S. tridactylus*.

Table 1

Measurements of *Subhyracodon hesperius*, M.C.Z. 9118

Measurements are given in millimeters throughout this paper.
A-P, antero-posterior; Tr, transverse; d, deciduous; e, estimated; r, across roots.

symphysis to angle of jaw	e405	
length of symphysis	106.4	
depth of jaw below P_2	65.4	
depth of jaw below M_2	71.8	
	right	left
mesio-distal I_1 alveolus	7.4	8.5
bucco-lingual I_1 alveolus	5.4	7.6
length (crown) of I_2 right	39.3	
(between worn tip and end of enamel)		
width (mesio-distal) I_2 right	20.3	
P_1-M_3	e171	
P_2-M_3	e165.5	
P_{1-4}	r67.4	
P_{2-4}	r61.9	
M_{1-3}	e101.2	
	e103, if complete	
A-P, P_1	r6.0	
A-P, P_2	r14.9	
A-P, P_3	r19.1	
A-P, P_4	r23.4	
A-P, M_1	e28.5	
Tr, M_1	24.2	
A-P, M_2	36.3	
Tr, M_2	24.6 (talonid)	
	26.5 across trigonid	
A-P, M_3	e42.3	
Tr, M_3	e22.0 (talonid)	
	25.5 across trigonid	

SUBHYRACODON OCCIDENTALIS (Leidy), 1850
Figure 3 *A*, *B*

Rhinoceros hesperius Leidy, referred specimen, Leidy 1868; Leidy, 1869, p. 388; Whitney, 1879, pp. 234-244, 253; Stock, 1933, p. 22.

Specimen. M.C.Z. No. 9119, a left ramus of a young individual with dP_{2-4} and M_1 in place and the unerupted trigonid of M_2 (Fig. 3, *A*, *B*).

Horizon and locality. Tertiary "auriferous gravels," presumably Oligocene, Douglas (or Douglass) Flat, Calaveras Co., California.

Leidy several times mentioned the association of this specimen (which he referred to *R. hesperius*) with *Archaeotherium superbum* (Leidy, 1868; 1869, p. 388; 1873, p. 218). Whitney (1879, pp. 243-244, 253) gave a brief description, chiefly quoted from Leidy's manuscript notes, with some information on the geology of the site (pp. 129, 243-244, 253, 527). An old paper label on the specimen bears the number "82." The ramus was preserved in a coarse sandstone with numerous volcanic fragments. Some of the grains and small pebbles are angular. The tooth pattern was largely obscured by this matrix and is only now adequately exposed for comparison. M_1 had just fully erupted; the trigonid is somewhat worn but the talonid barely so; the crown of the trigonid of the unerupted M_2 is near the cingulum of M_1. Some fracturing artificially elongates and narrows the teeth. This specimen is obviously not the other side of M.C.Z. No. 9118, the type of *S. hesperius*, an adult, nor could it be from the same individual as M.C.Z. No. 9120-9121, also an adult. The type of preservation resembles M.C.Z. No. 9120-9121 but differs definitely from M.C.Z. No. 9118.

Leidy's assignment of M.C.Z. No. 9119 to his *Rhinoceros hesperius*, which has not previously been questioned, was a natural one. However, it is clearly incorrect, since the deciduous and permanent premolar series of rhinoceroses in general, and of any given primitive rhinoceros, in particular, are of comparable length; whereas *S. hesperius*, M.C.Z. No. 9118, has a length of 67.4 for P_{1-4}, and M.C.Z. No. 9119 a length of 91.8 for dP_{2-4} (measured along the roots in both cases). Nor are the comparable parts of M_1 closely similar.

Comparison with *Trigonias*, *Subhyracodon* and *Diceratherium* seems warranted. No deciduous lower dentition of *Trigonias* was available for comparison; dP_{2-4} of M.C.Z. No. 9119 occlude readily with a deciduous upper dentition, A.M.N.H. No. 46000. However, the external and internal cingula of M_1 are too heavy for

Trigonias, thereby conforming to the *Subhyracodon — Diceratherium* pattern. Inside this line, the deciduous premolars show significant resemblances to those of *Subhyracodon occidentalis, S. tridactylus* and *Diceratherium annectens.* A.M.N.H. No. 1112, a calf jaw preserving alveoli of two deciduous incisors (apparently dI_{2-3}), the alveolus of dP_1, dP_{2-4} in place and M_1 not erupted, from the *Protoceras* beds, assigned, doubtless correctly, on the basis of size and stratigraphic level, to *Subhyracodon tridactylus*, agrees generally with M.C.Z. No. 9119. However, assignment of M.C.Z. No. 9119 to this species is ruled out by the character of M_1, which is markedly larger and coarser and has heavier cingula in A.M.N.H. No. 1112. Deciduous lower premolars referred to *D. annectens* are generally somewhat more specialized than M.C.Z. No. 9119, but four calf specimens, Y.P.M. No. 11066, a collective number, including a left ramus with dP_{3-4}, another with dP_{1-2}, and a third with dP_{3-4}, and a fourth consisting of both rami with dP_{2-3} in place and dP_4 erupting, show rather close resemblance to M.C.Z. No. 9119. However, assignment to *D. annectens* is improbable on the basis of the character of M_1 which, while otherwise the same size, is higher crowned in *D. annectens* than in M.C.Z. No. 9119.

Fig. 3. *Subhyracodon occidentalis* calf, M.C.Z. No. 9119. *A*, left ramus with dP_{2-4} M_{1-2}, lateral view, position of M_2 slightly shifted; *B*, left dP_{2-4} M_{1-2}, crown view; both x .598.

On the other hand, resemblance to *Subhyracodon occidentalis* calves is close throughout. The closest match is with A.M.N.H. No. 38938, a calf skull and jaws of *S. occidentalis* from the lower Oreodon beds. These two specimens are in almost exactly the same stage of tooth eruption and wear, and the agreement is extremely close. The teeth of M.C.Z. No. 9119 have been somewhat elongated and narrowed by crushing, accounting for some slight differences in measurement. Otherwise, agreement is extraordinarily close, including the enclosed basin in the talonid of dP_2 of M.C.Z. No. 9119, which is usually open in *S. occidentalis*, as it is on left dP_2 of A.M.N.H. No. 38938, but it is closed on the right dP_2. It also compares well, although not quite so closely, with A.M.N.H. No. 534, a calf skull and jaws also referable to *S. occidentalis*, from the Oreodon beds (Osborn 1898, pp. 155-156, fig. 46). It occludes well with A.M.N.H. Nos. 534, 1125 and 11297, all calf upper dentitions referable to *S. occidentalis*. As no other comparisons are equally close, this ramus is reidentified as *Subhyracodon occidentalis*. The character of the lower teeth is shown in Figure 3 *A*, *B*, and the measurements are given below.

TABLE 2

Measurements of *Subhyracodon occidentalis*

		Subhyracodon occidentalis		*Subhyracodon occidentalis*	
	M.C.Z. No. 9119	A.M.N.H. No. 38938		A.M.N.H. No. 534	
	Left	Right	Left	Right	Left
A-P, $dP_{2\text{-}4}$	93.7		e82.7	88.9	87.8
A-P, dP_2	26.0	20.9	20.8	25.6	24.4
Tr, dP_2	11.3	12.1	11.9	14.1	13.3
A-P, dP_3	35.1	33.5	32.6	33.4	33.1
Tr, dP_3		17.0	16.9	18.6	17.9
A-P, dP_4	33.9	29.9	31.3	33.7	33.1
Tr, dP_4	16.7	17.9	17.5	19.6	18.9
A-P, M_1	37.0	32.7	33.3		
Tr, M_1	15.9	21.3	21.0		

I submitted a sample of the matrix removed from M.C.Z. No. 9119 to Dr. Donald E. Savage of the University of California, who reports (letter dated February 25, 1955): ". . . regarding the matrix from the *Subhyracodon*, M.C.Z. 9119 from Douglass Flat. I conferred with two geologists who have mapped that region and have a better picture of the lithologic units. They agree that the matrix was at least partly volcanic debris in origin; however, this isn't particularly definitive because volcanics below the Valley Springs formation (rhyolite debris) and Mehrten fm. (andesitic debris) are known from the 'auriferous gravel' complex. It was no special surprise to them that a specimen of Oligocenish age had some volcanic matrix."

To summarize the stratigraphic indications, *Archaeotherium superbum*, discussed above, and this *Subhyracodon occidentalis* calf, M.C.Z. No. 9119 constituting the Douglass Flat local fauna (Wood *et al.*, 1941, p. 19) indicate an Orellan (middle Oligocene) age.

SUBHYRACODON KEWI Stock, 1933
Figure 4

"Probably *R. hesperius*," Leidy, 1869, pp. 231-232; Stock, 1933, p. 23.

Specimens. M.C.Z. No. 9120, an M^3, left, and M.C.Z. No. 9121, a partial left M^2 (Fig. 4), with fragments of other teeth, all apparently from a single individual.

Horizon and locality. "Reported to have been discovered in association with human and equine remains in Calaveras Co., California" (Leidy, 1869, p. 231).

Fig. 4. *Subhyracodon kewi*, M.C.Z. Nos. 9120-9121, left M^{2-3}, crown view, x 1.

I was struck by this material in the M.C.Z. collections, labelled "*Diceratherium hesperium* (Leidy); ?California (Miocene); J. D. Whitney Coll.," without further data. Comparison of these teeth with Leidy's accurate description (1869, pp. 231-232) leaves no possible doubt that he was referring to these teeth. A visit to the California Institute of Technology collections convinced me that these teeth are referable to *Subhyracodon kewi* Stock (1933, pp. 17-23, Pls. 1-3). Every identifiable morphological character appears to be identical, particularly the incipiently *Aphelops*-like crochet of M^3 and the somewhat greater pinching off of the protocone than is usual in *Subhyracodon*, superimposed on a generally *Subhyracodon* aspect. The molars seem to be nearly or entirely devoid of internal cingula. Some of these points suggest how a particular species of *Subhyracodon* could have been the start of the *Aphelops* line, and strengthen my previous suspicion that *Aphelops* is a descendant of *Subhyracodon* rather than an immigrant from the Eastern Hemisphere. Whether this line passes through any species of *Diceratherium* or, rather more probably, through something that, if known at all, has been called *Diceratherium* on the basis of inadequate material, must be left for future evidence to decide.

The two molars, M.C.Z. Nos. 9120 and 9121, with identical color and mode of preservation, are regarded as having belonged to the same individual as (with M^3 in a not quite fully erupted position) their interproximal wear facets fit exactly.

TABLE 3

Comparative Measurements of *Subhyracodon kewi*

	Subhyracodon kewi referred	*Subhyracodon kewi* (after Stock, 1933)		
	M.C.Z. Nos. 9120 and 9121	C.I.T. No. 1205	C.I.T. No. 1221	C.I.T. No. 1222
	Left	Type	Paratype	Paratype
Tr M^2	e41	36.3	40.4	39
A-P M^3	32.9		35.4	35.2
Tr M^3	36.9		40.1	35.1

These measurements show that there is nothing unreasonable in referring M.C.Z. Nos. 9120-9121 to *S. kewi*, Stock. The locality is sufficiently uncertain so that stratigraphic inferences should not be based on these teeth. From the morphology of the teeth, the first probability would be Whitneyan age, or, if not, early Arikareean, i.e., somewhere near what is currently taken as the Oligocene-Miocene boundary.

These teeth have a unique claim to fame. The famous Calaveras human skull was collected in 1866 (Whitney, 1867 a). Leidy (1869, p. 231) refers to these rhinoceros teeth as "reported to have been discovered in association with human and equine remains in Calaveras Co., California." In view of Leidy's undeviating exactitude, this statement must have been based on Whitney's authority, perhaps softened with a note of caution on Leidy's part. Apparently, Whitney, himself (1867 a, 1868, 1879) never recorded this association in print. Whitney found himself in a highly controversial position regarding Calaveras man (cf. Bret Harte's [1902] poem "To the Pliocene Skull" and Stewart [1931]). While Whitney (1879) still considered the

Calaveras skull as Pliocene, he never mentioned the rhinoceros teeth. Perhaps Whitney realized that these teeth proved too much, that, as "Miocene," in his terminology, or "Oligocene or early Miocene," in modern terminology, their association with the Calaveras skull, if any, must have been accidental or intrusive. These teeth, then, are the closest to a concrete foundation for Bret Harte's lines:

"Then Brown he read a paper, and reconstructed there,
From these same bones, an animal that was extremely rare."

These lines are often quoted by vertebrate paleontologists but seldom identified with "The Society Upon the Stanislaus" much less with Whitney's arbitrary stand. The situation caught the public fancy when Harte's poem first appeared in the San Francisco News Letter and National Advertiser in September, 1868, under the title "Proceedings of the Academy of Sciences at Smith's Crossing, Tuolumne County" (Stewart, 1931, p. 177). Frederic Remington's contemporary sketch (Harte, 1902, facing p. 132) shows Remington himself smiling beside the preposterous restoration. The determined man with beard and glasses, his hand clenched on the manuscript, doubtless "Brown of Calaveras" could be a thinly disguised portrait of Whitney. Mark Twain appears gleeful in the upper left with John Muir just below, and Bret Harte on Brown's right. Besides numerous miners convulsed in mirth, there are other portraits whose identity is probably gone forever.

SUBHYRACODON PLANICEPS (Scott and Osborn), *nomen dubium*

Figure 5; Plate, *lower figure*

Hyracodon planiceps Scott and Osborn, 1887, pp. 170-171.
Hyracodon planiceps, Hay, 1902, p. 641.
Caenopus mitis?, Scott, 1941, p. 794.

Type. M.C.Z. No. 6608, a partial calf skull, with dP^{2-4} right and left.

Horizon and locality. Collected by Samuel Garman, in the White River group, July 1880, without data as to level, doubtless from the Oligocene Big Badlands of South Dakota.

The original description of this specimen and of the species proposed for it, was based on an extraordinary misconception, namely, that the teeth are true molars, representing a young adult. Hence the infantile characters, such as the flat dorsal surface of the skull (thus "*planiceps*") and the widely separated temporal ridges, were regarded as specific characters. It was never figured and has never been redescribed. Making the obvious correction that this is a calf skull, with dP^{2-4}, it is certainly not *Hyracodon* nor any hyracodont, but an Oligocene true rhinoceros, i. e., one of the Caenopinae. This was implied by Matthew (*in* Osborn, 1909, p. 105). It is not *Trigonias* because of the heavy internal cingula; the pattern seems too primitive for *Diceratherium*. *Amphicaenopus* calves appear to be unknown; its size could not debar it with certainty from *Amphicaenopus platycephalus*, though there is no positive evidence to support this assignment. Scott (1941, p. 794) tentatively refers *H. planiceps* to *Caenopus mitis*, which is impossible on size alone, as well as highly improbable from the tooth characters, such as the heavy cingula.

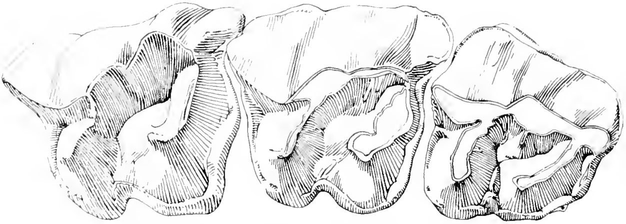

Fig. 5. *Subhyracodon planiceps*, type M.C.Z. No. 6608, right dP^{2-4}, crown view, x 1.

There is no trace of M^1; dP^{2-3} are moderately worn, dp^4 is unworn. All the close resemblances of M.C.Z. 6608 are to *Subhyracodon* calves. There are general resemblances to *S. occidentalis* calves in the American Museum collections (e.g., A.M.N.H. No. 534, see Osborn, 1898, Pl. 13, fig. 6), but some differences are present. The teeth of M.C.Z. No. 6608 are somewhat larger and "heavier" looking, about in proportion to the dental advance of adult *S. tridactylus* over *S. occidentalis*. A sharp, distinct, cuspule juts up in the median valley of dP^2; buccal to the internal cingulum. Right dP^2 has an incipient double crochet on its metaloph. The premolars have internal cingula, briefly interrupted by the hypocones. The minute remaining fragments of the matrix are more suggestive of the Poleslide (upper) Member of the Brule (Bump, 1956) than of the Scenic Member.

TABLE 4
Measurements of M.C.Z. No. 6608

	Right	Left
A-P, dP^{2-4}	88.7	89.6
A-P, dP^2	28.5	28.0
Tr, dP^2	33.0	31.3
A-P, dP^3	28.8	28.3
Tr, dP^3	36.0	e35
A-P, dP^4	33.0	31.5
Tr, dP^4	35.5	34.8

If I were only guessing, the most probable specific allocation would be with *Subhyracodon tridactylus* since, in addition to the reasons already given, dP^{2-4} is about the length of P^{2-4} of this species. It also occludes satisfactorily with A.M.N.H. No. 1112, a calf lower dentition referred to *S. tridactylus.* If this synonymy could be conclusively demonstrated, *S. planiceps* (Scott and Osborn, 1887) would have priority over *S. tridactylus* (Osborn, 1893) by six years. However, the following alternative interpretations are possible: (1) an extra large, aberrant *S. occidentalis;* (2) *S. occidentalis metalophus,* if that form is valid; or (3) the unknown calf of *Amphicaenopus platycephalus.* Even if one concludes that *S. planiceps* is more probably conspecific with *S. tridactylus* than not, it would be pedantic and a definite disservice to everyone to try to substitute a nearly forgotten name, based on a calf skull of unknown stratigraphic level, for a long established name, based on a nearly complete adult skeleton from a known level. The soundest treatment, therefore, seems to be to refer "*Hyracodon*" *planiceps* to *Subhyracodon,* with fair probability, but to consider it a *nomen dubium.*

A notice has been submitted to the Secretary of the International Commission on Zoological Nomenclature proposing the suppression of *Hyracodon planiceps* Scott and Osborn as a *nomen dubium,* stating the case as herein given. This notice has been accepted for publication in the Bulletin of Zoological Nomenclature.

DICERATHERIUM sp. cf. D. ARMATUM (Marsh), 1873

Figure 6 *A, B*

". . . a small rhinoceros," Woodworth and Wigglesworth, 1934, pp. 26, 85, 159-160.

Specimen. M.C.Z. No. 10883, the cast of a left permanent upper premolar, without ectoloph, interpreted as P^2 of *D.* sp. cf. *D. armatum.*

Horizon and locality. Miocene deep blue clay at base of greensand, Gay Head Cliff, Martha's Vineyard, Mass.

This specimen has stratigraphic and geographic significance only: it extends the range of *Diceratherium* farther east than New Jersey (Wood, 1939) and indicates, in the famous Gay Head Cliff section, an equivalent of the continental early Miocene (Arikareean). The specimen is referred to *Diceratherium* because of the incipient double crochet on the metaconule and the ribs which descend from protocone and metacone to join as a sort of half-hearted mure. This combination of characters could hardly be found except in *Diceratherium* and no characters contradict this assignment. The anteroposterior dimension along the middle of the tooth is 28.9 mm. The tooth is tentatively identified as P^2 of *Diceratherium* sp. cf. *D. armatum*. Daniel Vincent collected this interesting specimen about 1913, and gave it to M.C.Z. on January 26, 1918. It later went to the Boston Society of Natural History in an exchange arranged by Prof. J. B. Woodworth. Since then it has eluded the most careful hunting. Fortunately, M.C.Z.'s presumably accurate cast, No. 10883, remains to document its former existence. Woodworth and Wigglesworth (1934, pp. 26, 85, 159, 160) cite it briefly as a mid-Tertiary rhinoceros tooth, omitting description or identification with the implication that it was examined and described by Glover M. Allen. However, Allen apparently never published a description.

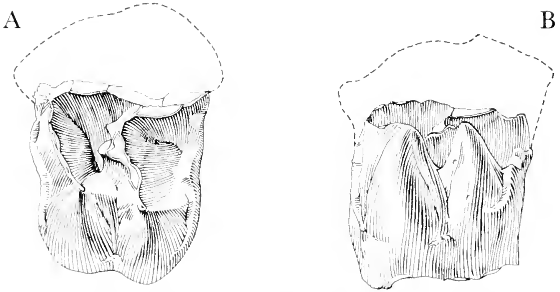

Fig. 6. *Diceratherium* sp. cf. *D. armatum*, M.C.Z. No. 10883, cast of a damaged left upper premolar, apparently P^2, from Martha's Vineyard, Mass.; *A*, crown view, *B*, lingual view, x 1.

TABLE 5
Comparative Measurements of *Diceratherium armatum*

	M.C.Z. No. 10883	*Diceratherium armatum* type, Y.P.M. No. 10003	
	Left	Right	Left
A-P, P^2	28.9	29.1	27.7
Bottom of "post fossette" to internal margin of tooth	20.5	18.3	18.4

Family HYRACODONTIDAE

HYRACODON NEBRASKENSIS (Leidy)

Figure 7

Hyracodon major Scott and Osborn, 1887, p. 170.

Type. P. U. No. 10001, miscellaneous postcranial bones of a large *Hyracodon*, inseparable from *Hyracodon nebraskensis.*

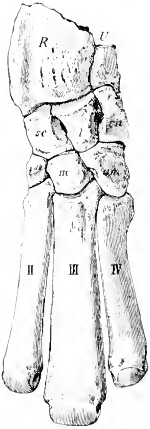

Fig. 7. *Caenopus* cf. *mitis,* M.C.Z. No. 11703, anterior aspect of left manus. Basis for type description of *Hyracodon major,* hitherto unpublished drawing by Rudolph Weber, x .325.

Type description. Based on M.C.Z. No. 11703, a partial left manus referable to *Caenopus, sensu stricto*, possibly to *Caenopus mitis* (Fig. 7).

Scott and Osborn (1887, p. 170) state that the "type of this species is a fairly complete skeleton in the Princeton Museum."

According to Sinclair (1922a, p. 477) and the Princeton University Catalogue of Fossil Vertebrates, this specimen is P.U. No. 10001, which, while a large individual, is not beyond the present known size range of *Hyracodon nebraskensis*, and is completely without other distinctive characters. Nevertheless, Scott and Osborn based their entire type description on M.C.Z. No. 11703, a specimen consisting of a partial left manus of a true *Caenopus* which agrees closely with P.U. No. 11418, the right manus attributed, probably correctly, to *C. mitis* by Scott (1941, Pl. 88, figs. 3 and 3a). Allen (1931, p. 286) concluded, with some reason, that, despite the clear statement by Scott and Osborn, M.C.Z. No. 11703 is really the type, since they based their description exclusively on it. This treatment would make *H. major* a probable synonym of *C. mitis*. I prefer the alternative interpretation, treating the Princeton specimen as the type, and assigning *H. major* to synonymy with *H. nebraskensis*, which would make M.C.Z. No. 11703 a misidentified referred specimen, now re-assigned to *Caenopus*, probably to *C. mitis*. In either case, *Hyracodon major* is a junior synonym, whether of *H. nebraskensis* or of *Caenopus mitis*.

TABLE 6
Measurements of manus, M.C.Z. No. 11703

	Greatest length	Functional median length
Mtc. IV	102	110
Mtc. II	115	119
Mtc. III	126	99

Family AMYNODONTIDAE

METAMYNODON Scott and Osborn, 1887

Cadurcopsis Kretzoi, 1942.

Genotype. *Metamynodon planifrons* Scott and Osborn, 1887, pp. 165-169.

The genus *Metamynodon* will be given only a summary treatment here because an extended discussion of the Amynodontidae is in preparation. This genus has occupied an equivocal position because of numerous misconceptions in print. The following short discussion should clarify the more puzzling aspects pending the release of the more thorough treatment.

Scott (1941) treats this genus satisfactorily, limiting himself essentially to *M. planifrons*. It has been unfortunate that the most widely known purported illustration of the crown view of the upper dentition of *M. planifrons* (Osborn, 1898, fig. 10) actually represents the type specimen of *Amynodon intermedius*

Osborn (1889), redrawn somewhat incorrectly from a photograph. In conjunction with the damaged teeth of the type specimen of *M. planifrons*, this illustration seems to have misled various workers (especially foreign paleontologists forced to rely on illustrations) as to the dental characters of *Metamynodon*.

METAMYNODON PLANIFRONS Scott and Osborn, 1887

Figure 8; Plate, *upper figure*

Amynodon aff. *intermedius*, Pavlow, 1893, pp. 37-42.
Metamynodon rex Troxell, 1921a, p. 24.
Cadurcopsis dakotana, Kretzoi, 1942, pp. 139-148.

Type. M.C.Z. No. 9157, a good skull with badly damaged teeth; a left ramus, M.C.Z. No. 9157, is tentatively associated with the skull; *paratype*, M.C.Z. No. 11931, the right ramus of a different individual.

Horizon and locality. "White River Miocene" (= Oligocene), collected by Samuel Garman, 1880-1881. All specimens of this species of known locality and level are from the *Metamynodon* sandstones or stream channels, in the lower part of the Scenic Member of the Brule (early Orellan or early middle Oligocene) of the Big Badlands of South Dakota.

Diagnosis. $I\,\frac{3\text{-}2}{2\text{-}1}$, $C\,\frac{1}{1}$, $dP\,\frac{3}{3}$, $P\,\frac{3}{2\text{-}(1)}$, $M\,\frac{3}{3}$; incisors most often $\frac{2}{1}$; large everted canines, crowns triangular in section; upper premolars relatively small and often incipiently trilophodont, with a high posterior cingulum simulating a third transverse crest; P^4 almost pear-shaped in outline, bulbous internally, instead of rectangular, an effect further accentuated by crown and interstitial wear; P_3 degenerate, suggestive of anterior premolars of other rhinoceroses, whether P_1 or P_2; molars, upper and lower, hypsodont, buccally, when unworn, and brachyodont or nearly so lingually, enormously overshadowing the premolars in size; outline of unworn M^1 keystone shaped, becoming rectangular with prolonged wear; lower molars unusually elongated, with posterior crescent relatively flattened; size range (in millimeters): P^2-M^3, 200-230; $P^{2\text{-}4}$, 60-67; $M^{1\text{-}3}$, 140-170; P_3-M_3, 203-217; $M_{1\text{-}3}$, 160-174, differences in length largely a function of wear; short broad skull with very short face; short nasals; dorsally convex sagittal crest; wide zygomata.

Scott (1941) treats the genus by a full discussion of the species *M. planifrons*, without much reference to the type specimen, except for figure 140 and page 848 which deal with the region of the anterior nares. Scott and Osborn (1887, pp. 165-169) gave an excellent description of the type, for the time; their figures 7 and 8, giving lateral and anterior views, are still sufficiently accurate, as far as they go. The description does not indicate which characters of the lower jaw are taken from M.C.Z. No. 9157, supposedly part of the type, and which from M.C.Z. No. 11931, the paratype. The skull has been moderately crushed, dorsoventrally, with the dorsal surface shoved somewhat to the right, accounting for the general difference in appearance from many specimens which have been crushed laterally. Scott's restoration (1941, Pl. 91, fig. 1a) of the *M. planifrons* skull, in anterior view, with crushing compensated for, accords with present knowledge. The most unsatisfactory part of the type description is the account and illustration (Scott and Osborn, 1887, fig. 9) of the dentition, as shown in the ventral view of the skull. This must have been largely conjectural, since the teeth are seriously damaged, and the valleys of the teeth were filled with matrix until my visit to Harvard in August, 1954. A new and more accurate figure of the cheek teeth is given here (Fig. 8).

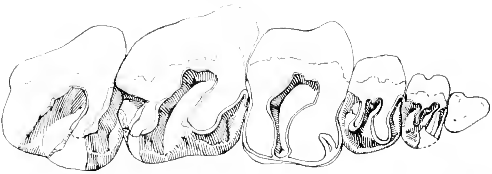

Fig. 8. *Metamynodon planifrons*, type M.C.Z. No. 9157, left P^2-M^3; P^3, M^1, and M^2 slightly restored from opposite side, x .372.

SUMMARY

1. The fossil mammals of the Whitney collection from the California "auriferous gravels" are all of mid-Tertiary age, with the probable spread only from Orellan to Whitneyan (middle to upper Oligocene). The extreme possible spread would be from Chadronian to Arikareean.
2. *Subhyracodon kewi* is a reasonable structural ancestor for *Aphelops*.
3. The rhinoceros tooth from Martha's Vineyard is assigned to *Diceratherium* cf. *armatum*, an Arikareean (lower Miocene) guide fossil.

4. The Harvard rhinoceros types of Scott and Osborn are redescribed and discussed. *"Hyracodon major"* is a synonym of *Hyracodon nebraskensis*. *"Hyracodon planiceps"* is placed in *Subhyracodon* as a *nomen dubium*, and the characters of *Metamynodon planifrons* are clarified.

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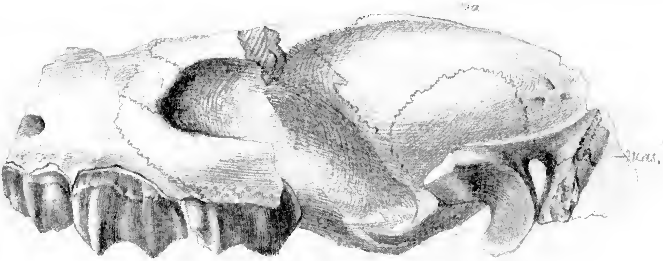

Plate. *Upper figure, Metamynodon planifrons*, type, M.C.Z. No. 9157, dorsal view of skull, x .20. Photograph by Frank White.

Lower figure, Subhyraeodon planiceps, type, M.C.Z. No. 6609, lateral view of skull, x .50. Hitherto unpublished pencil drawing by Rudolph Weber, approved May 18, 1887.

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THE STRUCTURE OF THE CHOANAE OF THE EMYDINAE (TESTUDINES, TESTUDINIDAE)

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No. 4 — *The Structure of the Choanae of the Emydinae (Testudines, Testudinidae)*

By Thomas S. Parsons[1]
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Cambridge 38, Massachusetts

INTRODUCTION

A variety of ridges, flaps, and papillae are found along the lateral margin of the choanae in many turtles although apparently they have been described only in the Cheloniidae (see Parsons, 1958, for a discussion of that family). The present study describes their occurrence and variation in the Emydinae and comments on the relation of these findings to the phylogeny of this group.

Originally, it was hoped that some account of the histology of emydine choanal papillae and a discussion of their possible functions could be included. However a rather quick check of the former showed that a careful study using special techniques would be necessary before any valuable conclusions could be reached. The gross morphology gives no positive clues to the function of the various structures described below. On the negative side, the flap which is frequently present is almost certainly not a valve between the nasal and oral cavities since it is almost never large enough to close off the entire choanal opening (two specimens of *Pseudemys floridana*, out of sixty-nine seen, are the only possible exceptions). A detailed histological study of this area would thus be a very valuable contribution towards an understanding of the choanal flaps and papillae.

No attempt was made to survey the choanae of the other subfamilies of the Testudinidae although several testudinines were observed. Some variation was observed, but it does not appear to be as great as in the Emydinae. In none of the eight specimens seen, which represent the genera *Chersina*, *Geochelone*, *Gopherus*, *Kinixys*, and *Malacochersus* (terminology that of Loveridge and Williams, 1957), was a papilla found, although the other conditions found in emydines were present.

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the collections under their care: Mr. C. M. Bogert and Dr. S. B. McDowell (American Museum of Natural History), Dr. E. E. Williams (Museum of Comparative Zoology), Dr. D. M. Cochran (United States National Museum), and Drs. N. E. Hartweg and R. E. Etheridge (University of Michigan Museum of Zoology). Dr. McDowell also provided a sketch of the choanae of *Pseudemys scripta hiltoni* and checked several specimens for me, and Dr. Hartweg very kindly examined several specimens of *Pseudemys*. The discussion owes much to the many helpful comments and suggestions of Dr. Williams who has also critically read the manuscript for me. Thanks are also due to Dr. M. C. Parsons who made the drawings and the histological preparations.

OBSERVATIONS

Before presenting the findings of this study, several qualifications and warnings are necessary. First, the sample used, while quite large, is not really adequate either in respect to the number of forms or the number of examples of each form. Representatives of all but two of the genera (*Annamemys* and *Batagur*)[1] and of approximately three-quarters of the recognized species and forms (104 out of 137) were seen. However, the sample was five or more for only thirty-four of these forms, and in thirty-seven cases only one specimen was available. Little effort was made to check the identifications of the specimens, so it is quite possible that some of them are misidentified. The condition of the specimens was frequently not ideal for this study; in some cases the mouth was only partly open and the choanae difficult to see, and in others the preservation of the area was not good. A final problem is that the categories used, which are described below, are arbitrary and not, in all cases, sharply distinct. Thus any future study will almost certainly uncover errors in the present work, especially concerning those forms only one specimen of which was checked.

For descriptive purposes it is convenient to recognize four somewhat arbitrarily separated morphological configurations of the lateral margin of the choana. In the most complex of the four, there is a flap (rarely a ridge) of variable size attached along the lateral choanal margin; near the anterior end of the flap there is a single, generally rather small papilla (see Figs.

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[1] The nomenclature used throughout is that of Mertens and Wermuth (1955), except that *Emys* is here considered to be monotypic (*E. orbicularis*), with *E. blandingii* being placed in the genus *Emydoidea* as suggested by Loveridge and Williams (1957), and *Hardella indi* is recognized as a valid species.

1 A and B). In most, but not all, specimens possessing such a papilla, the flap is folded ventrally so that it lies along the lateral margin of the choana rather than projecting medially into the opening. A second pattern resembles that described above in possessing a lateral flap, but there is no papilla (see Figs. 1 C and D). The flap is generally slightly smaller than in the first type and usually projects medially into the choana although it is sometimes folded ventrally. In the third group the lateral margin of the choana is marked by a ridge rather than a flap (see Figs. 1 E and F); the distinction between a ridge and a flap is quite subjective and, in many cases, the structure could equally well be called either one. In the figures almost no difference is visible, but probing of the actual specimens does reveal

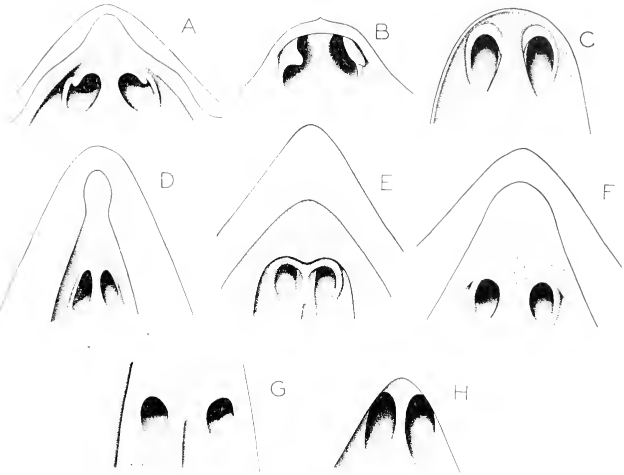

Fig. 1. The choanae of various emydines seen in ventral view to show the four patterns described in the text. The entire palate is not shown. In B, the papilla is folded ventrally on the right side as in the actual specimen; it is shown extended medially on the left. A: *Cyclemys dentata* (MCZ 29573). B: *Hardella thurjii* (MCZ 4002). C: *Hieremys annandalii* (MCZ 4103). D: *Graptemys kohnii* (MCZ 29091). E: *Terrapene ornata* (MCZ 32395). F: *Clemmys marmorata* (MCZ 7877). G: *Malayemys subtrijuga* (MCZ 43083). H: *Graptemys barbouri* (MCZ 46255).

some degree of distinctness. The ridge may project either medially or ventrally. Finally, in the fourth type there is no special structure along the lateral border of the choana (see Figs. 1 G and H). Thus the four patterns may be characterized by the presence, respectively, of a papilla, of a flap, of a ridge, or of nothing at the lateral choanal margin.

The distribution of these four patterns is shown in the following list. The number after each form gives the number of specimens which have been seen, and the letters refer to the patterns, with A for the possession of a papilla, B for a flap, C for a ridge, and D for the absence of such structures. A capital letter is used for the predominant condition while lower case letters indicate less common or variant patterns which were observed.

Callagur borneoensis (1)	A			
Chinemys reevesii (6)		B	c	
Chrysemys picta picta (12)		B	c	
Chrysemys picta bellii (8)		B	c	d
Chrysemys picta dorsalis (1)		B		
Chrysemys picta marginata (2)		B		
Clemmys bealei (1)			C	
Clemmys caspica caspica (2)			C	
Clemmys caspica rivulata (3)		b	C	
Clemmys guttata (15)		b	C	d
Clemmys insculpta (8)		B	c	
Clemmys japonica (1)		B		
Clemmys leprosa (2)		b	C	
Clemmys marmorata marmorata (3)			C	
Clemmys marmorata pallida (8)		b	C	
Clemmys muhlenbergii (6)		b	C	d
Clemmys nigricans (2)			C	
Cuora amboinensis (4)		B		
Cuora flavomarginata (1)		b	C	
Cuora trifasciata (2)		B		
Cyclemys dentata (5)	A			
Deirochelys reticularia (8)			C	d
Emydoidea blandingii (4)		b	C	d
Emys orbicularis (6)			C	d
Geoclemys hamiltonii (1)	A			
Geoemyda annulata (10)		b	C	d
Geoemyda areolata (2)			C	
Geoemyda funerea (3)	A			
Geoemyda pulcherrima pulcherrima (4)		B	c	

Geoemyda pulcherrima incisa (5)		B		
Geoemyda punctularia punctularia (7)	A	b		
Geoemyda punctularia diademata (1)	A			
Geoemyda punctularia lunata (1)	A			
Geoemyda punctularia melanosterna (1)	A			
Geoemyda rubida perixantha (1)			C	
Geoemyda spengleri japonica (2)			C	
Goemyda spinosa (1)				D
Geoemyda tcheponensis (1)	A			
Geoemyda trijuga thermalis (1)			C	
Graptemys barbouri (19)		B	c	d
Graptemys geographica (5)		B	c	
Graptemys kohnii (5)		B		
Graptemys oculifera oculifera (2)		B		
Graptemys oculifera flavimaculata (1)		B		
Graptemys oculifera nigrinoda (2)		B		
Graptemys pseudogeographica pseudogeographica (11)	a	B	c	
Graptemys pseudogeographica ouachitensis (1)		B		
Graptemys pseudogeographica sabinensis (1)		B		
Graptemys pseudogeographica versa (1)		B		
Graptemys pulchra (3)		B		
Hardella indi (1)	A	b		
Hardella thurjii (9)	A			
Hieremys annandalii (1)		B		
Kachuga tecta tecta (2)	A			
Kachuga tecta tentoria (1)[1]	A			
Kachuga trivittata (1)	A			
Malaclemys terrapin terrapin (8)		b	C	d
Malaclemys terrapin centrata (1)			C	
Malaclemys terrapin macrospilota (1)				D
Malaclemys terrapin pileata (3)			C	
Malaclemys terrapin rhizophorarum (2)		B		
Malayemys subtrijuga (2)				D
Morenia ocellata (1)	A			
Notochelys platynota (1)		B		
Ocadia sinensis (3)		B		
Orlitia borneensis (1)		B		
Pseudemys callirostris (1)		B		
Pseudemys dorbigni (1)		B		
Pseudemys floridana floridana (5)	A			
Pseudemys floridana concinna (3)	A			

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[1] MCZ 3233; re-identified by Dr. S. B. McDowell.

Pseudemys floridana hieroglyphica (1)	A			
Pseudemys floridana hoyi (7)	A			
Pseudemys floridana mobilensis (18)	A			
Pseudemys floridana peninsularis (13)	A			
Pseudemys floridana suwanniensis (21)	A			
Pseudemys floridana texana (1)	A			
Pseudemys grayi (1)		B		
Pseudemys nelsoni (6)	A			
Pseudemys ornata ornata (2)		B		
Pseudemys ornata cataspila (9)		B	c	
Pseudemys ornata nebulosa (1)	A			
Pseudemys rubiventris rubiventris (24)	A			
Pseudemys rubiventris bangsi (1)	A			
Pseudemys scripta scripta (10)		B		
Pseudemys scripta elegans (16)		B		
Pseudemys scripta gaigeae (2)		B		
Pseudemys scripta hiltoni (4)	a	b		D
Pseudemys terrapen angusta (1)		B		
Pseudemys terrapen decorata (2)		B		
Pseudemys terrapen decussata (29)		B	c	
Pseudemys terrapen felis (1)		B		
Pseudemys terrapen granti (4)		B		
Pseudemys terrapen malonei (6)		B		
Pseudemys terrapen plana (1)		B		
Pseudemys terrapen stejnegeri (2)		B		
Pseudemys terrapen vicina (4)		B		
Siebenrockiella crassicollis (4)		B		
Terrapene carolina carolina (19)		b	C	
Terrapene carolina bauri (3)			C	
Terrapene carolina major (4)			C	
Terrapene carolina triunguis (8)			C	
Terrapene mexicana mexicana (1)			C	
Terrapene nelsoni klauberi (3)			C	
Terrapene ornata ornata (31)			C	

It is obvious from inspection of the preceding list that there are numerous cases in which intraspecific variation occurs. It should also be noted that there can be considerable variation within one of the four categories. The variable forms are here discussed briefly, considering them in alphabetical order by genera.

Chinemys: The variation in *C. reevesii* is primarily the result of the arbitrary distinction between a flap and a ridge; four specimens have a small flap and two a large ridge, but the difference is very small.

Chrysemys: The possession of a flap is clearly the typical condition in *C. picta;* it occurs in nineteen of the twenty-three specimens. Of the remaining four, three have only a ridge and one has nothing. It is possible, as in all cases in which the variant pattern is essentially a reduction of the normal, that the variant specimens originally showed the typical pattern, but have been damaged or improperly preserved.

Clemmys: This genus seems typically to possess a ridge, but it varies greatly in size, ranging from a small flap to nothing. In most cases this variation is overemphasized by the arbitrary distinction between a flap and a ridge. Four of the five *C. caspica,* three of the eight *C. insculpta,* one of the two *C. leprosa,* and seven of the eleven *C. marmorata* possess a ridge, while the others have a small flap. The variation is greater in *C. guttata* (one with a flap, eleven with a ridge, and three with nothing) and *C. muhlenbergii* (one with a flap, three with a ridge, and two with nothing).

Cuora: The single specimen of *C. flavomarginata* shows a condition almost on the line between a ridge and a flap; despite the fact that the other species of this genus appear to possess a flap, it seems slightly on the ridge side in this one case.

Deirochelys: Five specimens of *D. reticularia* have a very small ridge, while in one there is a larger ridge and in two there is nothing.

Emydoidea: *E. blandingii* appears to be a rather variable species on the basis of only four specimens; one possesses a flap, two have ridges, and one shows nothing.

Emys: In two specimens of *E. orbicularis* there is nothing, but the other four possess ridges, very faint in one case but well developed in the others.

Geoemyda: This genus shows remarkable variability between species, but the sample seen is too small to permit any detailed consideration of intraspecific variation. Seven of the ten specimens of *G. annulata* possess ridges of variable size while one has a flap and two have nothing. In *G. pulcherrima* there is little actual variation; six specimens have small flaps and two have large ridges. The ninth one has a larger flap. Finally, in *G. punctularia* there is a very small flap which, in nine of the ten specimens, possesses a small papilla.

Graptemys: The possession of a fairly small flap appears to be characteristic of this genus, at least in small specimens. In

G. barbouri a sizable series is available, and there is some variation which seems to be correlated with the size of the animal. The fourteen specimens with a carapace length of less than 120 mm. possess flaps, generally quite small ones, a specimen with a carapace about 120 mm. long has only a ridge, and the four larger ones have nothing. In *G. geographica*, three specimens with carapace lengths of less than 110 mm. have small flaps while ones of 90 and 220 mm. have only ridges. Fourteen specimens of *G. pseudogeographica* with carapace lengths of less than 150 mm. have flaps, while one of two specimens about 200 mm. long has a flap and the other only a ridge. One of the smaller specimens possesses a small papilla (the only case in fifty-two examples of this genus). All the other species are represented only by small specimens with carapace lengths of under 120 mm.

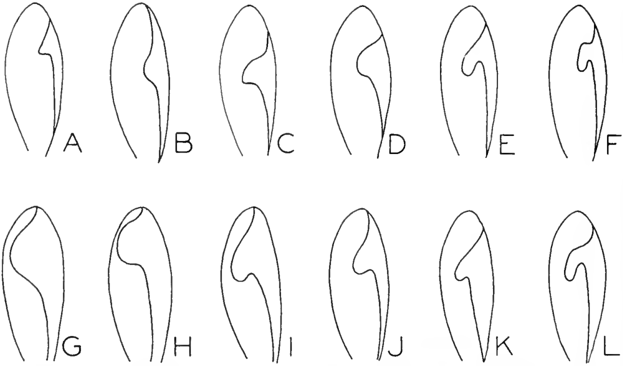

Fig. 2. Outlines of the right choanae of *Pseudemys floridana* to show variation in the size and shape of the flap and papilla. In all cases the flap has been drawn as extended medially. A: *P. f. mobilensis* (MCZ 1662). B: *P. f. suwanniensis* (MCZ 54677). C: *P. f. peninsularis* (MCZ 43849). D: *P. f. peninsularis* (MCZ 43850). E: *P. f. mobilensis* (MCZ 1663). F: *P. f. suwanniensis* (MCZ 43030). G: *P f. mobilensis* (MCZ 1659). H: *P. f. suwanniensis* (MCZ 54667). I: *P. f. hieroglyphica* (MCZ 16487). J: *P. f. suwanniensis* (MCZ 54676). K: *P. f. mobilensis* (MCZ 1651). L: *P. f. mobilensis* (MCZ 1648).

Hardella: In the one specimen of *H. indi* (kindly examined for me by Dr. McDowell), a papilla was present on one side, but not on the other which had only a flap.

Malaclemys: A ridge is apparently typical of *M. terrapin* and is found in nine of the fifteen specimens; four have small flaps and two show nothing.

Orlitia: In the one specimen of *O. borneensis* (examined by Dr. McDowell), the margin of the flap is slightly scalloped; such a pattern is otherwise unknown among the emydines.

Pseudemys: This genus falls into two main sections, the *P. floridana* plus *P. rubiventris* series, and the *P. scripta* series. All one hundred specimens of the first group (representing all the forms recognized by Mertens and Wermuth, 1955) possess papillae. There is considerable variation in the size of both the flap and the papilla and in the shape of the latter, as is shown in Figure 2. This variation does not appear, on the basis of the sample seen, to be related to either the size of the animal or the race to which it belongs, although *P. rubiventris* may tend to have a slightly smaller flap than *P. floridana.* The *P. scripta* series as a whole is characterized by the possession of a flap of variable and frequently rather small size, but no papilla; such a pattern is found in eighty-nine of the ninety-seven specimens of this series. Two specimens (one *P. ornata catespila* and one *P. terrapen decussata*) have only a ridge, while another *P. terrapen decussata,* shown in Figure 3 A, presents a completely anomalous picture. In the last specimen, the entire choana is covered by a thin membrane pierced on one side by two small circular openings and on the other side by a single such hole. Finally, *P. ornata nebulosa* and *P. scripta hiltoni* do not follow the pattern set by the remainder of the series. In the type and

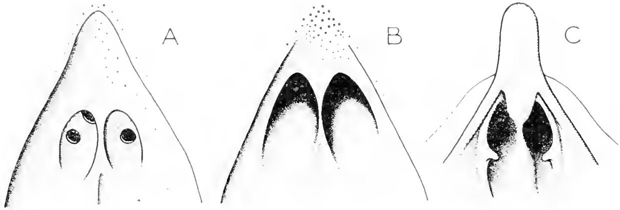

Fig. 3. A: Ventral view of the choanae of an anomalous specimen of *Pseudemys terrapen decussata* (MCZ 56437). B and C: Ventral views of the choanae of two specimens of *Pseudemys scripta hiltoni* to show the variation in this form (B, MCZ 46678; C, AMNH 63748).

only example of the former used in the present study (kindly examined for me by Dr. Hartweg), there is a papilla present. Two of the four specimens of *P. scripta hiltoni* also possess papillae, on both sides in one case and on only one side in the other, while the other two specimens (including the type examined by Dr. Hartweg) have no sign of any special structure along the lateral choanal margin (see Figs. 3 B and C). The degree of variation seen in this form is thus greater than that found in any other emydine examined.

Terrapene: All the species of this genus typically have a ridge which varies greatly in size in all cases where there is an adequate sample. Two of the thirty-four specimens of *T. carolina* possess small flaps and are the only exceptions. In *T. ornata,* five of the thirty-one specimens have a small bump near the anterior end of the ridge; it does not closely resemble the papillae found in other genera and is probably an independent specialization. However it could be a vestigial papilla.

DISCUSSION

This discussion deals primarily with the phylogenetic implications of the various choanal structures described above. It must, of course, be emphasized that no one character can ever provide a reliable basis for any phylogenetic scheme; many different and unrelated characters must be considered. However, such a detailed treatment is beyond the scope of this paper, and the following remarks can be no more than suggestive. An added liability is that, of necessity, only living forms are treated so that dendrograms rather than true phyletic trees must be used. In considering the relationships between genera, Williams' dendrogram of the emydines (Loveridge and Williams, 1957, p. 185) forms the most convenient starting point. It is reproduced as Figure 4 with the various symbols that he used for different characters omitted, but with the choanal configurations noted after each genus in parentheses. The letters used are the same as those in the list in the descriptive section (A for papilla present, B for flap, C for ridge, and D for nothing). Only what is believed to be the typical pattern or patterns is indicated; rarer variants are omitted.

The first problem to be faced is the determination of which choanal configuration is to be considered most primitive, and which specialized. In the absence of any knowledge of the functional significance of the various structures, this is not easy and the conclusions cannot be considered absolutely reliable. The lack of any *obvious* function suggests that the most complex pattern, that of a papilla plus flap, may be primitive, and that the evolutionary picture within the emydines is one of loss,

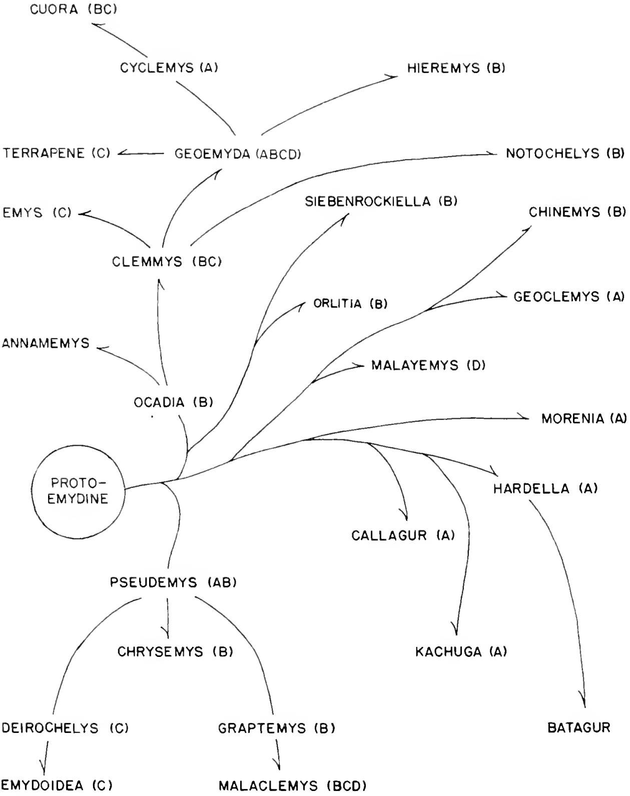

Fig. 4. Dendrogram of emydine relationships (modified from Loveridge and Williams, 1957). The letters in parentheses indicate the choanal configurations typical of the various genera, with A for the presence of a papilla, B for a flap, C for a ridge, and D for nothing.

occurring at different rates and in different groups of related genera. If the reverse is assumed, that the papilla is a specialized structure evolved within certain emydines, then the diversity of the forms in which it occurs appears to require that it has evolved in parallel fashion in several lines. While such a parallel development is certainly possible, its acceptance is somewhat embarrassing in the absence of any functional explanation.

A more profitable way to attack the problem is to see which choanal pattern is found in those genera previously thought to be primitive. However, the results again cannot be considered conclusive; the primitiveness of one structure in an animal is no proof that another structure in that animal is also primitive. As shown in Figure 4, the unicarinate series (*Pseudemys* and allies) fits in well with the theory that the presence of a papilla is primitive. However, in the remaining forms (the tricarinate series), no pattern is discernible. One subgroup, the Asian river turtles (*Callagur* and allies), consistently possesses a choanal papilla (*Hardella indi* is a minor exception); while these forms do show certain characters which Williams considered to be primitive, they have exaggerated such traits (strong buttressing of the shell, wide triturating surfaces, and maxillary triturating ridges) to an extreme and presumably quite specialized condition. The other subgroups are less consistent and hence harder to discuss. One interesting point can be noted: the genera showing the smallest development of choanal papillae or flaps are almost certainly *not* primitive. The only genus characterized by the total absence of any choanal structure, *Malayemys*, has a very specialized skull with a well developed secondary palate and no waist to the united pterygoids. *Terrapene* and *Emys*, which have only a ridge, both possess a hinged plastron which is certainly not a primitive trait.

Hence it seems most probable that the primitive emydine possessed a well developed choanal flap with a papilla, but that this has been reduced to a greater or lesser degree in many of the Recent genera. Such will be assumed, despite its unproven nature, throughout the remainder of the discussion.

As stated above, if the presence of a papilla is considered primitive, the unicarinate series of genera (*Pseudemys* and allies) shows a consistent pattern of simplification in Williams' dendrogram, so that the nature of the choanae may be used as additional evidence for his views. Two of the subgroups of the tricarinate assemblage are uniform and hence this character is of no use in a study of their relationships: all of the Asian river turtles (*Callagur* and allies) seen in the present study possess a papilla, and both *Orlitia* and *Siebenrockiella* have a flap. In the latter case the irregularity of the margin of the flap in *Orlitia* appears to be a specialization, but it is a very minor one and probably cannot be used to deny the more primitive nature of that genus (the characters in which it is shown as more primitive than *Siebenrockiella*, by Williams, are the presence of moderate buttressing of the shell, the presence of ridges on the maxillary triturating surface, and the position of the humeropectoral suture).

The other subgroups are more complex and present definite problems. In the case of *Malayemys*, *Geoclemys*, and *Chinemys*, I believe that the choanal structures probably reflect the true order of specialization, with *Geoclemys* most primitive and *Malayemys* most advanced. This belief is based on an examination of the skulls of all three forms (in the case of *Geoclemys* drawings of the skull kindly furnished by Dr. McDowell were also used to advantage). The following are the specializations noted within these genera: enlargement of the maxillary triturating surface (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the latter); straightening of the lateral margin of the pterygoid with a reduction of the waist of the united pterygoids (least in *Chinemys* and most in *Malayemys* with *Geoclemys* closer to the former); reduction of the ventral projection of the articular process of the quadrate (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the former); reduction of the interorbital fenestra (least in *Chinemys* and most in *Malayemys* with *Geoclemys* closer to the former); reduction of the orbitonasal foramen (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the latter); narrowing of the incisura columellae auris (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the former); enlargement of the mandibular triturating surface (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the former); and enlargement of the coronoid process (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the latter). In Williams' dendrogram, the only characters in which these three genera are noted as differing are in the position of the humeropectoral suture, which crosses the entoplastron only in *Chinemys*, and in the partial loss of the tricarinate pattern in *Chinemys;* in both these cases *Chinemys* is considered to be more specialized than the other two genera.

A larger and more difficult subgroup is that containing *Ocadia*, *Clemmys*, and their allies. Here the pattern of choanal types appears to be nearly random. *Ocadia* is unique in this subgroup in the possession of two characters considered by Williams to be primitive: moderate buttressing of the shell and ridging of the maxillary triturating surface. Possibly this form and *Annamemys* should be removed from the base of the larger subgroup and made into another small independent subgroup. However, such a suggestion would have to be substantiated by the study of other characters before it could be proposed with any confidence, especially since Williams' diagram is a dendrogram and not a true phyletic tree; the Recent *Ocadia sinensis* is certainly *not* ancestral to the whole assemblage of genera. The other problem within this subgroup concerns the position of *Geoemyda*. This genus is exceedingly variable, with different species showing all four types of choanal structure. If *Geoemyda* were to be considered more primitive with *Clemmys* descended from it rather than the reverse, then the remainder of the subgroup would present a consistent pattern. However, especially in view of the trend towards reduction or loss of the temporal arcade in *Geoemyda*, this certainly cannot be more than suggested as one possibility on the evidence given in this paper. Further discussion of this subgroup without the consideration of numerous other characters does not appear to me to be profitable and is, therefore, not attempted.

Finally, the situation within the genus *Pseudemys* deserves some comment. The *P. floridana* plus *P. rubiventris* series always possess a choanal papilla and hence are presumably primitive. In the *P. scripta* series only a flap is present typically; the only significant exceptions are in populations found in western Mexico (the other three exceptions, two specimens with ridges and one anomalous case, can hardly be considered significant). I have not seen any *P. ornata nebulosa*, but the type was checked by Dr. Hartweg and found to possess a papilla. Papillae are also present in two of the four specimens of the type series of *P. scripta hiltoni* (the specific distinction of *P. ornata* and *scripta* is open to serious doubt; see Williams, 1956). These data obviously suggest that these forms may be the most primitive of the *scripta* series. However, the situation is not simple; *hiltoni* varies greatly, and in two of the specimens (including the type) there is no trace of any papilla, flap, or ridge along the lateral choanal margin. One possible theory is that *nebulosa* is primitive and that *hiltoni* represents an intergrade population between *nebulosa* and *P. scripta gaigeae*. Under such conditions the great variation seen in *hiltoni* would not be too surprising. Unfortunately, not only is my sample of these forms small, but the total knowledge of *hiltoni* is minimal and whether or not it actually does intergrade with other forms is completely unknown.

The most recent survey of the entire *scripta* series is that by Williams (1956). He used plastral pattern as a primary character. Based on this, he recognized three subseries, one (*scripta*) in the United States, a second (*ornata*) in Mexico, Central and South America, and the West Indies, and a third ("intermediate populations") in northern and western Mexico. He further suggested that the *ornata* subseries may be the most primitive since its plastral pattern resembles that of the *P. floridana* series plus species in certain closely related genera. Both *hiltoni* and *nebulosa* have patterns not closely comparable with those of the remaining forms although they may, in certain cases at least, resemble each other. Although the plastral pattern of the type of *hiltoni* is quite distinctive, there is considerable variation in the type series (four specimens; see Carr, 1942), and definite statements on the affinities of this form do not appear to be possible. Thus, while the evidence of choanal structure and that of plastral patterns seems to be somewhat at variance, both would indicate a close relationship between *hiltoni* and *nebulosa*. Beyond that, definite conclusions cannot safely be drawn.

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THE NERVOUS SYSTEM OF *GELASTOCORIS OCULATUS* (FABRICIUS) (HEMIPTERA-HETEROPTERA)

By Margaret C. Parsons
Harvard Biological Laboratories

PRINTED FOR THE MUSEUM
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September, 1960

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No. 5 — *The Nervous System of Gelastocoris oculatus (Fabricius) (Hemiptera-Heteroptera)*

BY MARGARET C. PARSONS[1]
Harvard Biological Laboratories

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INTRODUCTION

The Gelastocoridae are predaceous, shore-dwelling Heteroptera whose appearance and characteristic means of locomotion have earned them the common name of "toad bugs." Along with the other littoral families Ochteridae and Saldidae, they occupy an important place in theories of the evolution of the totally aquatic and semi-aquatic Heteroptera. The littoral families are believed to represent a stage in the evolution of the aquatic Heteroptera from terrestrial forms. In spite of the importance of the shore-dwelling bugs in phylogenetic theories, very little is known of their anatomy, especially of their internal morphology. In two previous papers the author has described the skeleton and musculature of the head (Parsons, 1959) and thorax (Parsons, 1960) of *Gelastocoris oculatus* (Fabricius), an insect which can be obtained in large numbers and is easily kept in the laboratory. The present paper is a continuation of the work on the anatomy

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of this species. It is hoped that these morphological studies will reveal evidence which may shed some light upon the phylogenetic position of the Gelastocoridae.

The literature on the heteropteran nervous system is quite extensive. Most authors have dealt mainly with the external appearance of the nervous system, primarily of the brain and the subesophageal ganglion. Their accounts included little or no histological description, and did not treat the thoracic nerves in any detail. Among these are the works of Brandt (1878; many Heteroptera), Marshall and Severin (1904; *Ranatra*), Titschack (1928; *Cimex*), Hamilton (1931; *Nepa*), Malouf (1933; *Nezara*), Rawat (1939; *Naucoris*), Bickley (1942; *Nezara* and *Arilus*), Sprague (1956; *Hydrometra*), and Akbar (1958; *Leptocorisa*). A very detailed description of the brain of *Corixa*, with some histological observations, was presented by Benwitz (1956). Papers dealing with the histology of the brain, along with the external appearance of the nervous system, include those of Pflugfelder (1936-37; many Heteroptera), Graichen (1936; *Nepa*), and Johansson (1957; *Oncopeltus*). The last author also illustrated, in some detail, the paths of the thoracic nerves. Wigglesworth (1959) has recently published an account of the histology of the central nervous system of *Rhodnius*. The endocrine glands of a variety of Heteroptera have been studied by Nabert (1913) and Cazal (1948). More recently, Junqua (1956) has described these glands in *Hydrocyrius*, and Nayar (1956a and b) has studied the fine structure of the endocrines of *Iphita*.

I am indebted to the members of the C. V. Riley Entomological Society of Columbia, Missouri, and to Mr. Edwin P. Marks of Washburn University, who supplied the gelastocorids used in this study. I also wish to thank Prof. Frank M. Carpenter of Harvard University, Dr. Isabelle B. Sprague of Mount Holyoke College, and my husband, Dr. Thomas S. Parsons of Harvard University, for their advice and help with the preparation of the manuscript. This study was made possible by a Grant-in-Aid from the Sigma Xi-RESA Research Fund.

MATERIALS AND METHODS

The nervous system was studied both by means of dissections and sectioned material. The dissections were made in 80 per cent alcohol under a stereoscopic microscope, using insects preserved in alcoholic or aqueous Bouin's solution, Kahle's solution, or 100 per cent formalin, and stored in 80 per cent alcohol. In order to make the nerves stand out from the muscular and fatty tissue in the dissections, a few drops of Delafield's hematoxylin were introduced into the area to be studied, by means of a fine pipette. The excess stain was then drawn off after a few seconds. Overstaining by this method was remedied by dipping the dissection for a few seconds into a 1 per cent solution of hydrochloric acid in 70 per cent alcohol.

Nine adults, one fifth-instar nymph and one fourth-instar nymph were sectioned for histological study. In all but one, the entire body was sectioned; only the head was used in the case of one of the adults. Frontal, transverse, and sagittal sections were cut at 7 μ by means of the Peterfi method. Most of the insects were preserved immediately after moulting, while the exoskeleton was still soft, to facilitate sectioning. The material was fixed in alcoholic or aqueous Bouin's solution, F.A.A., or 10 per cent formalin, and stained with Delafield's hematoxylin and eosin or with Mallory's triple connective-tissue stain.

CENTRAL AND PERIPHERAL NERVOUS SYSTEM

Gross Morphology

The central nervous system of *Gelastocoris,* like that of other Hemiptera, shows a high degree of fusion of the ganglia. It consists of four main ganglionic masses, the *brain* (*BR*), the *subesophageal ganglion* (*GS*), the *prothoracic ganglion* (*GPR*), and the *posterior ganglion* (*GP*) (Fig. 1). The last is formed by the fusion of the mesothoracic, metathoracic, and abdominal ganglia. The brain and subesophageal ganglion are closely connected by short, thick *circumesophageal connectives* and thus appear externally as a single mass, their boundaries being indistinct. The subesophageal and prothoracic ganglia are broadly joined, their connectives being fused medially. Dorsally there is no clear boundary between them (Fig. 1), although an indentation separates them ventrally and ventrolaterally (Fig. 2). Their boundary is also indicated by the point of entrance of two tracheoles (*TL*) which penetrate the ganglionic mass medially and run dorsoventrally between the prothoracic and subesophageal ganglia. A pair of long, thick *longitudinal connectives* (*LC*) runs from the prothoracic ganglion to the posterior ganglion (Fig. 1); these ganglia are clearly separated from each other.

The brain and most of the subesophageal ganglion lie within the head of the insect, while the prothoracic and posterior ganglia are located in the thorax. The longitudinal axis of the head

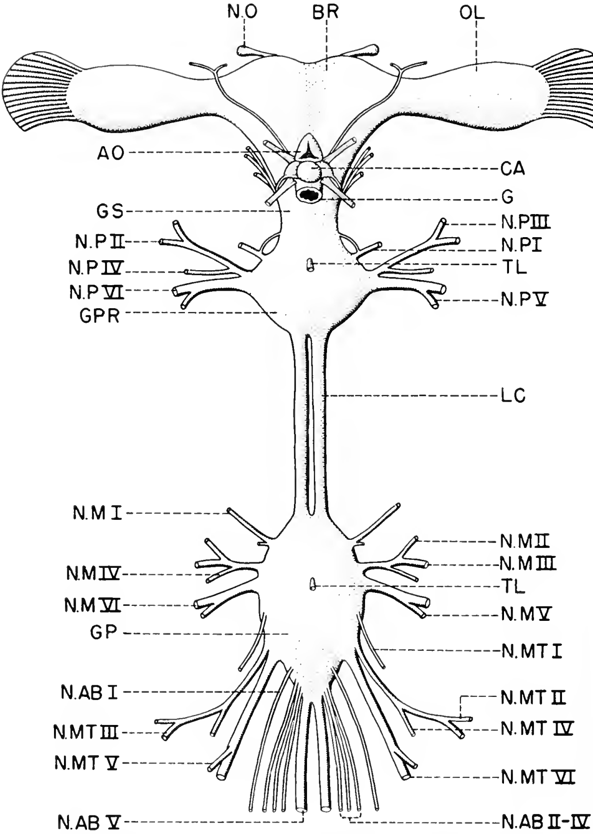

Fig. 1. Dorsal view of the nervous system of *Gelastocoris*, showing the bases of the main nerves. 30 X.

is roughly perpendicular to that of the body as a whole. For convenience in the following discussion, however, the directional terminology employed for all parts of the central and peripheral nervous system will be used in relation to the body as a whole.

Brain. The brain ("Oberschlundganglion" or "supra-esophageal ganglion" of many authors) consists predominantly of the *protocerebrum* (*P;* Fig. 3), with its conspicuous laterally projecting *optic lobes* (*OL;* Figs. 1, 2, 3). The latter are elongate, being separated from the central protocerebral lobes by a slight constriction. From the ends of the optic lobes the *nervi optici* (*N.OP*) ("Retina-fasern" of Pflugfelder, 1936-37) run to the compound eyes (the terminology of Johansson, 1957, is employed here; some authors, such as Graichen, 1936, have used the term "optic nerves" for the fibers running from the optic lobes to the central part of the brain). These nerves are separate, and not, as in many Gymnocerata described by Pflugfelder (1936-37), grouped into two main bundles. The strong development of the optic lobes may be correlated with the large size of the compound eyes; Pflugfelder (1936-37) noted that in the Hydrocorisae large lobes were associated with large compound eyes, and small lobes with small eyes.

A slight medial depression separates the protocerebral lobes dorsally and anteriorly. From the anterior surface of the protocerebrum, on either side of the midline, the two *nervi ocelli* (*N.O*) project towards the ocelli (Figs. 1, 2, 3).

The *deutocerebrum* (*D*) is much smaller than the protocerebrum. It lies posterior and ventral to the latter, and appears externally as a pair of swellings on either side of the gut (Figs. 2, 3, 5). From the anterior portion of each deutocerebral lobe a thick *nervus antennalis* (*N.A*) arises. This is one of the most conspicuous of all the nerves of the brain; it runs anterolaterally, extending across *M. retractor setae mandibularis primus* (*H10;* Fig. 6)[1] and passing between the two extrinsic muscles of the antenna, *M. levator scapi* (*H20*) and *M. depressor scapi* (*H21*). In this region it sends off short branches to those two muscles as well as a longer *nervus tegumentarius primus* (*N.TI;* Fig. 3) which runs dorsally and breaks up into many fine branches in the region just ventral to the optic lobes (only two of these branches are shown in Figures 3 and 6). Benwitz (1956) noticed a similar tegumentary nerve (her "N. tegumentarius 2") arising

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[1] In the figures, the cephalic and thoracic muscles are indicated by the numbers assigned to them in my two previous papers (Parsons, 1959, 1960). The numbers of the cephalic muscles are preceded by an "H".

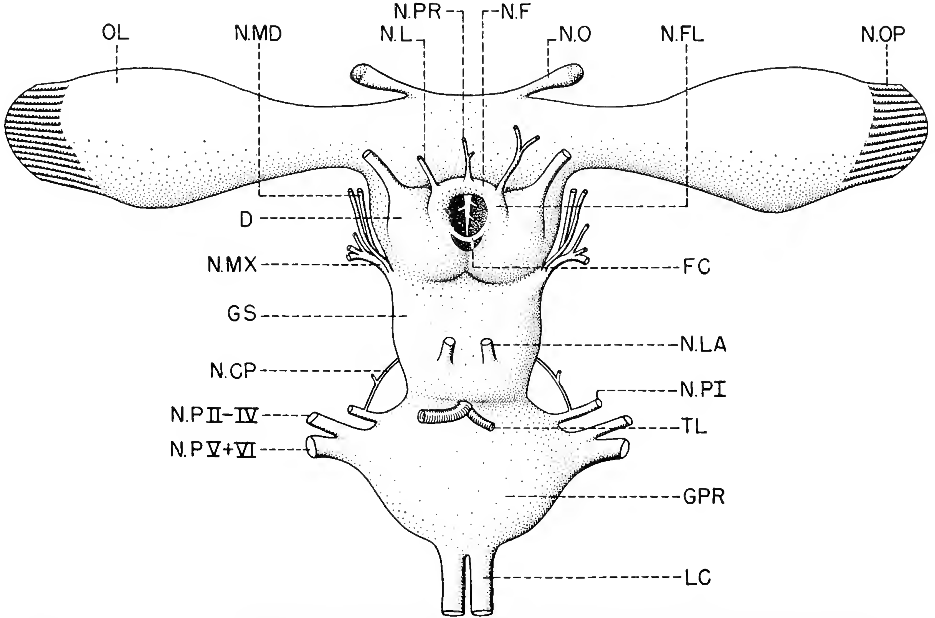

Fig. 2. Ventral view of the brain, subesophageal ganglion, and prothoracic ganglion, showing the bases of the main nerves. The gut has been removed.

from the antennal nerve of *Corixa*, and found that it, unlike the remainder of the antennal nerve, is composed of fibers whose central connections are in the circumesophageal connectives rather than in the deutocerebrum. The present author was unable to determine the origin of the first tegumentary nerve in sectioned material of *Gelastocoris*.

After innervating the extrinsic antennal muscles, the antennal nerve enters the antenna and runs through all four antennal segments, supplying the intrinsic muscles and sending numerous branches to the exoskeleton and to the intersegmental membranes. It is quite probable that the antennae of *Gelastocoris* possess sense organs similar to those described by Hüfner (1939) in the Hydrocorisae. Thus the antennal nerve is both sensory and motor in function. Many authors (Titschack, 1928; Pflugfelder, 1936-37; Benwitz, 1956; Johansson, 1957) have described the double nature of the antennal nerve in various Heteroptera, and Pflugfelder (1936-37) found that the fibers of this nerve separate after it enters the brain, some fibers going to the sensory portion and some to the motor portion of the deutocerebrum.

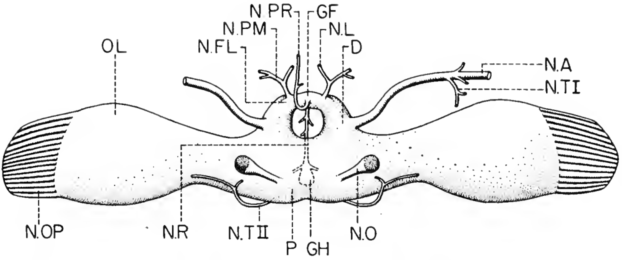

Fig. 3. Anterior view of the brain, showing the bases of the main nerves. The gut has been removed.

The *tritocerebrum* (*TR*) is much reduced. Sectioned material shows that it lies medial to the deutocerebrum (Figs. 19D, 21), but there is no clear separation between these two regions externally. Its location can be roughly estimated by the point of origin of the *nervi frontolabrales* (*N.FL;* Figs. 2, 3, 5). These short, thick nerves soon divide into the short *nervi frontales* (*N.F*) (the "frontal commissure" of Malouf, 1933) and the long, slender *nervi labrales* (*N.L*). The frontal nerves join, at the midline, in the *frontal ganglion* (*GF;* Figs. 3, 5); the labral nerve runs ventrally and soon gives off a side branch, *nervus protractoris mandibularis* (*N.PM;* Figs. 3, 6). The latter, in turn, bifurcates and sends branches to the two protractor muscles of the mandible, *Mm. protractores setae mandibularium primus* (*H8*) *et secundus* (*H9*) (Fig. 6). Both Benwitz (1956; *Corixa*) and Johansson (1957; *Oncopeltus*) found the mandibular protractors to be innervated by a nerve branching off from the labral nerve; the former author, however, stated that the fibers going to the mandibular protractors originate in the circumesophageal connectives while those going to the labral region come from the tritocerebrum. Graichen (1936; *Nepa*) reported

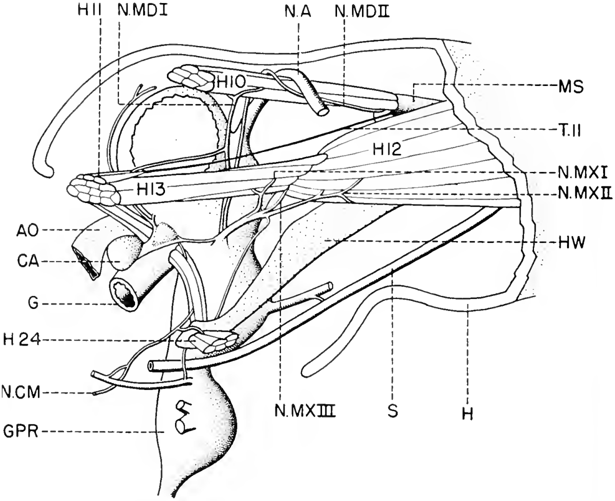

Fig. 4. Lateral view of the right side of the head, with the exoskeleton cut away to show the brain, subesophageal ganglion, and prothoracic ganglion in place. Only the bases of the antennal, labial, and prothoracic nerves are shown. The more medial cephalic muscles and skeletal structures are not shown. The optic lobe and ocellar nerve have been cut off near their bases.

that the mandibular protractors, like the retractors, are innervated by the mandibular nerve originating in the subesophageal ganglion.

After *nervus protractoris mandibularis* has branched off from *nervus labralis*, the latter passes into the lateral part of the food pump (*FP*) and runs ventrally between the cibarial dilator muscles and the side wall of the pump (Fig. 6). It appears to send short branches to at least the most ventral group of cibarial dilator muscles, *M. dilator cibarii primus* (*H14*). Benwitz (1956) has similarly found that the labral nerve supplies the cibarial muscles in *Corixa*. Ventral to the muscles of the pump, *nervus labralis* breaks up into a network of fine branches over the epipharyngeal plate (*EP*). It may be that there are sense organs in this region which are innervated by the labral nerve; Benwitz (1956) has reported the presence of a chemical "epipharyngeales Sinnesorgan" in the corresponding region in *Corixa*.

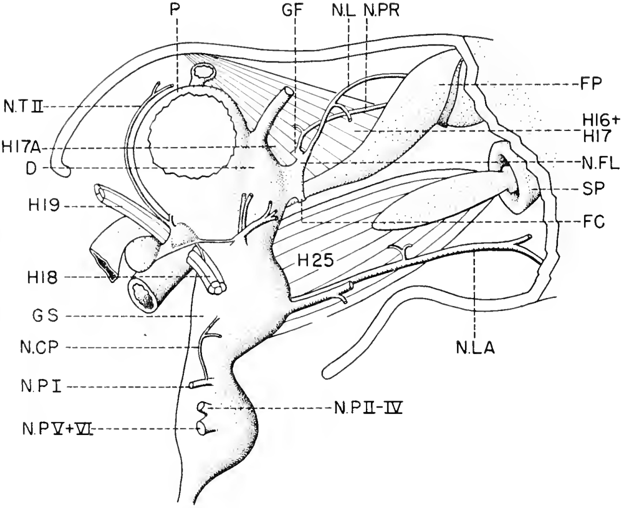

Fig. 5. Same view as Figure 4, with the stylets, the hypopharyngeal wing, and the lateral cephalic muscles removed to reveal the more medial muscles and skeletal structures. The nerves innervating the stylet muscles have been cut off near their bases.

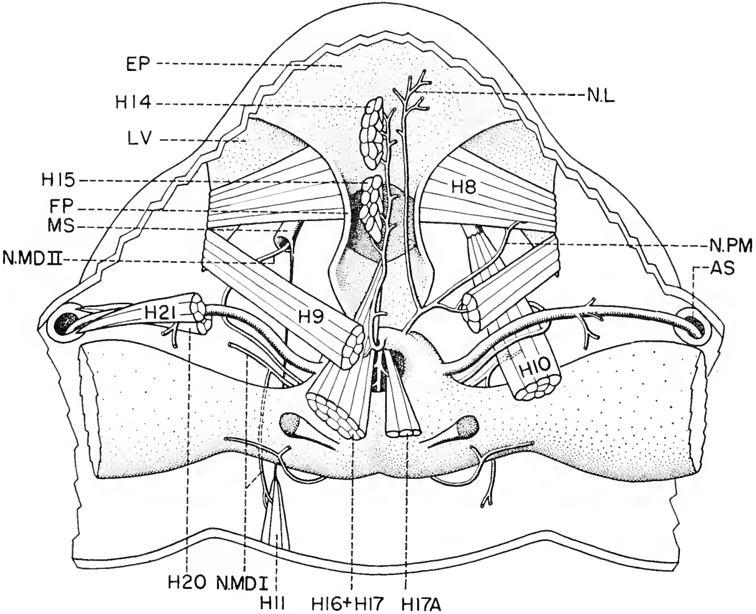

Fig. 6. Anterior view of the brain (same view as Fig. 3) shown in place in the head. The exoskeleton of the roof of the head, along with the optic lobes and the compound eyes, have been removed. Muscles *H11*, *H14*, *H15*, *H16*, *H17*, *H20*, *H21*, and the medial part of *H9* are omitted on the right side. *N.L* and part of *N.MDI* are omitted on the left side, along with Muscle *H10*. For unlabelled nerves, see Figure 3.

The tritocerebral part of the brain possesses two commissures. The more ventral of these (*FC*) runs between the bases of the *nervi frontolabrales* and passes beneath the gut just ventral to the brain (Figs. 2, 5). In histological sections its fibers appear to run to the frontal ganglion (Fig. 23), and it is, therefore, here termed the *frontal commissure*. It is the same as the "Dritthirnkommissur" of Titschack (1928), the "tritocerebral commissure" of Malouf (1933), Benwitz (1956), and Akbar (1958), the "Ringkommissur des Frontalganglions" of Graichen (1936), and the "free commissure" or "frontal commissure" of Johansson (1957). The last author doubted whether it is found in all bugs. A second commissure, the *tritocerebral commissure* (to be described later), unites the two tritocerebral lobes; it lies within the perilemma of the central nervous system and is therefore visible only in sectioned material.

Subesophageal Ganglion. The boundary between the brain and the subesophageal ganglion ("infra-oesophageal ganglion" of Marshall and Severin, 1904; "Unterschlundganglion" of many authors) is marked externally by only a slight indentation (Figs. 2, 5). The circumesophageal connectives are apparent histologically (*C;* Fig. 21), but they are not grossly distinct. From the anterolateral region of the subesophageal ganglion, just below the boundary between this ganglion and the brain, the nerves to the muscles of the stylets originate (Figs. 2, 4). In some individuals these nerves all seem to have a common base; in the majority of specimens, however, the mandibular nerves originate slightly anterior and ventral to the maxillary nerves.

The mandibular nerves, *nervi mandibulares primus et secundus*, lie very close together at their bases; in some specimens they join before entering the ganglion, while in others they are entirely separate. Both nerves extend anteriorly, passing between the brain and *M. retractor setae maxillaris* (*H13*). *Nervus mandibularis primus* (*N.MDI*) sends a branch dorsally to *M. retractor setae mandibularis secundus* (*H11*) and then goes to the posterior surface of *M. retractor setae mandibularis primus* (*H10*) (Figs. 4, 6). *Nervus mandibularis secundus* (*N.MDII*) extends medially and then anterolaterally across the latter muscle, running parallel to *nervus antennalis* (Figs. 4, 6). It then turns ventrally and goes to the base of the mandibular stylet (Fig. 4). Graichen (1936) has described, in *Nepa*, a single mandibular nerve which divides, one branch going to the mandibular retractor and the other to the base of the mandible. It is quite possible that the *nervus mandibularis secundus* of *Gelastocoris* innervates a proprioceptive organ at the base of the mandibular stylet, similar to the sensory organ described by Benwitz (1956) in *Corixa.* The single mandibular nerve of the latter insect sends a motor branch to the retractor muscle and a sensory branch to the proprioceptive organ; these branches are probably equivalent to the *nervi mandibulares primus et secundus,* respectively.

The maxillary nerves all have a common base. Although three main maxillary nerves could be distinguished in all the specimens examined, the general appearance of these nerves and their manner of branching showed considerable individual variation. The most common condition is shown in Figure 4; all three nerves separate at the same general level, *nervus maxillaris primus* (*N.MXI*) going anteriorly to the posterior surface of *M. retractor setae maxillaris* (*H13*), *nervus maxillaris secundus* (*N.MXII*) passing ventrally to supply *M. protractor setae maxillaris* (*H12*), and *nervus maxillaris tertius* (*N.MXIII*) running anteroventrally to the base of the maxillary stylet. A long, very slender maxillary nerve, usually appearing as a branch of *nervus maxillaris secundus,* extends dorsolaterally to the tip of the hypopharyngeal wing (*HW*); it was not possible to determine just what structures this nerve innervates. *Nervus maxillaris tertius* is probably associated with a maxillary proprioceptive organ, similar to that of *Corixa* as described by Benwitz (1956). In some individuals this nerve could not be located; in those specimens, however, there usually appeared to be an extra nerve to either the protractor muscle or the retractor muscle. Just before the common base of the maxillary nerves enters the subesophageal ganglion, the slender *nervus lateralis* (*N.LT*) from the corpus cardiacum fuses with it (Fig. 25); this nerve will be described later.

Graichen (1936) has described three maxillary nerves with a common base in *Nepa*, while Johansson (1957) figures two main maxillary nerves arising separately but close together in *Oncopeltus. Nervus maxillaris primus* probably represents the first and second maxillary nerves of Graichen (1936) and the first maxillary nerve of Johansson (1957), while *nervus maxillaris secundus* corresponds to the ''Nebenast'' of the first maxillary nerve of Graichen (1936), ''N. protractoris maxillaris'' of Benwitz (1956), and the second maxillary nerve of Johansson (1957). *Nervus maxillaris tertius* is similar to the third maxillary nerve of Graichen (1936).

A pair of thick, conspicuous *nervi labiales* (*N.LA*) arises from the ventral surface of the subesophageal ganglion (Figs. 2, 5) and runs ventrally into the labium. Before entering the latter, each nerve sends a short branch to the afferent salivary duct (*S;* Fig. 4) and, more ventrally, to *M. retractor pistilli* (*H25;* Fig. 5), the dilator muscle of the salivary pump. Ventral to the salivary pump (*SP*) it innervates the extrinsic labial muscles; it then enters the labium and sends branches to the intrinsic labial muscles.

A minute *nervus capitis-prothoracicus* (*N.CP*) arises from the lateral surface of the subesophageal ganglion, dorsal to the labial nerves, and runs posteriorly to join the first prothoracic nerve (*N.PI*) near the base of the latter (Figs. 2, 5). A fine side branch of the *nervus capitis-prothoracicus* extends laterally to the tip of the hypopharyngeal wing; whether or not it innervates any of the muscles originating on that structure could not be determined. Johansson (1957) has described a similar nerve, the "salivary gland nerve" of *Oncopeltus*, running from the lateral part of the subesophageal ganglion to the first prothoracic nerve and innervating the salivary glands. In *Gelastocoris*, however, *nervus capitis-prothoracicus* does not appear to go to the salivary glands.

Prothoracic Ganglion. The prothoracic ganglion ("first thoracic ganglion" of Hamilton, 1931, and Johansson, 1957; "Thorakalganglion" of Graichen, 1936) is merged anteriorly with the subesophageal ganglion. The longitudinal connectives between them, which can be seen histologically (Fig. 21), are fused medially, being separated only by a pair of tracheoles (*TL*) which pass between them in a dorsoventral direction. Externally the boundary between the two ganglia is marked ventrally and laterally by an indentation (Fig. 2); dorsally they merge without any apparent boundary.

The prothorax, like the mesothorax and metathorax, is innervated by six main nerves (Fig. 1). Most previous workers (Malouf, 1933; Johansson, 1957; Akbar, 1958) have recognized only three main nerves in each thoracic segment, grouping the second, third, and fourth, and the fifth and sixth nerves of the present work into two single nerves. Although, in all three thoracic segments of *Gelastocoris*, each of these two groups of nerves arises from a common base, it is more convenient, from the point of view of terminology, to consider them as five separate nerves rather than as branches of two nerves. The six main nerves of the three thoracic ganglia appear to show serial homology, each innervating comparable structures in their respective segments.

Figure 1 shows the relationship of the six prothoracic nerves to the prothoracic ganglion. *Nervus prothoracicus primus* (*N.PI*) is a slender nerve arising from the anterior part of the ganglion. It is similar to "nerve a" of Malouf (1933) and Akbar (1958); Johansson (1957) termed it the "first prothoracic nerve." Very close to its base it is joined by the previously described *nervus capitis-prothoracicus* from the subesophageal ganglion (Figs. 5, 7). It then passes ventral to two of the depressor and retractor muscles of the head, *Mm. prosterni primus et secundus* (*6* and *7*), sending a short branch to these muscles. In the region medial to the occipital condyle of the head it gives off a branch which joins a long nerve, *nervus capitis-mesothoracicus* (*N.CM*), running from the mesothorax and pass-

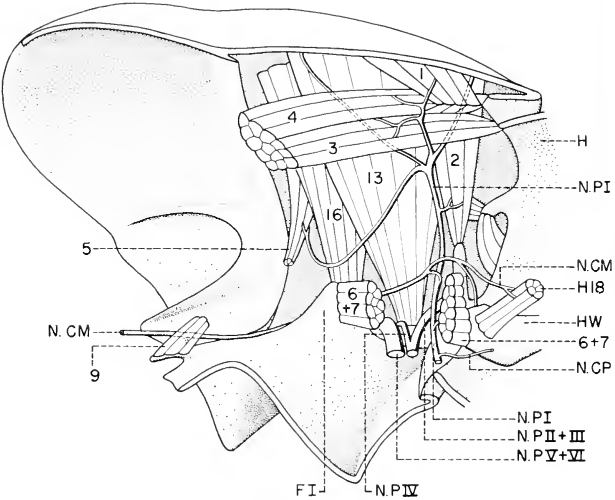

Fig. 7. Medial view of the left half of the prothorax, showing the innervation of the medial muscles. The posterior parts of the head and hypopharyngeal wing are shown in place. The dorsal parts of Muscles *H18* and *9*, and the middle part of Muscles *6* and *7* are omitted.

ing into the head (Figs. 4, 7). The latter nerve arises as a branch of the first mesothoracic nerve. It extends into the prothorax, passing lateral to and innervating one of the depressor muscles of that segment, *M. dorsoventralis* (*9*). After joining the ramus from the first prothoracic nerve it becomes quite fine and passes into the head. In most dissections it appears to innervate the muscle of the cephalic gland, *M. dilator oris glandulae capitis* (*H24*) and the ventral pharyngeal dilator muscle, *M. dilator postpharyngis ventralis* (*H18*), but this was not determined with certainty.

Nervus prothoracicus primus extends dorsally, sending a ramus to a depressor muscle of the head, *M. pronoti secundus* (*2*) and then dividing into four main branches (Fig. 7). Two of these run to the anterolateral and posterolateral regions of the pronotum, respectively. A third branch innervates three of the dorsal longitudinal prothoracic muscles, *Mm. pronoti primus, tertius, et quartus* (*1*, *3*, and *4*), while the fourth passes posteriorly to supply another of the prothoracic depressor muscles, *M. pronoti quintus* (*5*).

Nervi prothoracici secundus, tertius, et quartus arise together from the lateral part of the prothoracic ganglion (Fig. 1). These three nerves represent "nerve b" of Malouf (1933) and Akbar (1958), and the "second prothoracic nerve" of Johansson (1957). *Nervus prothoracicus quartus* (*N.PIV*) branches off quite soon from the common base, while *nervi prothoracici secundus et tertius* are joined as far as the anterior part of the coxal cavity. Then *nervus prothoracicus tertius* (*N.PIII*) enters the coxa while *nervus prothoracicus secundus* (*N.PII*) extends anterolaterally, anterior to the pleural apophysis (*PAI*) (Figs. 8, 9). The second prothoracic nerve sends a branch dorsally (Fig. 8) to innervate two of the promotor muscles of the foreleg, *M. noto-trochantinalis* (*13*; removed in Fig. 8) and *M. noto-coxalis primus* (*14*). More laterally it branches out to supply two of the muscles moving the head, *Mm. proepisterno-postoccipitales primus* (*10A*) *et secundus* (*10B*), along with another of the promotor muscles of the leg, *M. pleura-coxalis* (*17*; Fig. 8). The branch to the last muscle appears to divide, sending a fine ramus to the lateral surface of *M. noto-coxalis primus* (*14*).

Nervus prothoracicus tertius bifurcates just after entering the coxa (Fig. 10). One branch (*A*) passes through the anteromedial part of the coxa and divides to send rami to the lateral and anterior bundles of *M. coxa-trochanteralis lateralis* (*24*), which raises the trochanter. The second branch (*B*) of *nervus prothoracicus tertius* runs posteromedially, sending a ramus to the anterior bundle of *M. coxa-trochanteralis lateralis* and then joining *nervus prothoracicus sextus* (*N.PVI*) near the distal end of the coxa.

Nervus prothoracicus quartus bends into the medial region of the coxal cavity soon after its separation from *nervi prothoracici secundus et tertius* (Fig. 9). It appears to be joined by a very short branch to the base of *nervus prothoracicus sextus*. Just dorsal to the coxa and medial to the pericoxal membrane (*M*) it branches and innervates the extrinsic depressor muscles of the trochanter. One branch goes dorsally, passing between *M. pleura-trochanteralis* (*21*) and *M. noto-trochanteralis* (*20*) to innervate the two bundles of the latter muscle (*Mm. noto-trochanterales primus, 20A, et secundus, 20B*). A second branch runs directly to *M. pleura-trochanteralis* (*21*).

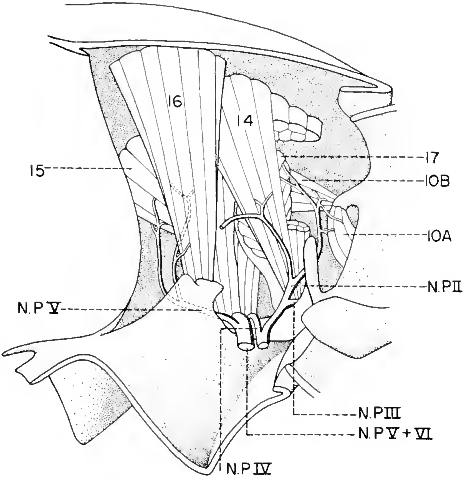

Fig. 8. Medial view of the left half of the prothorax (same view as Fig. 7), with the posterior prothoracic lobes omitted. *N.PI*, Muscles *H18*, *1*, *2*, *3*, *4*, *5*, *6*, *7*, *9*, and *13*, and part of Muscle *14* have been removed.

Nervi prothoracici quintus et sextus come off together from the lateral part of the prothoracic ganglion (Fig. 1). Their common base represents "nerve c" of Malouf (1933) and Akbar (1958) and the "third prothoracic nerve" of Johansson (1957). *Nervus prothoracicus quintus* (*N.PV*) (the "dorsal branch of the third prothoracic nerve" of Johansson, 1957) is a thick nerve, although not nearly as stout as *nervus prothoracicus sextus* (*N.PVI*). It passes posteriorly between the prothoracic furca (*FI*; Fig. 7) and the extrinsic leg muscles and then turns laterally (Figs. 8, 9). In the posterolateral region of the prothorax it first sends a long branch dorsally to *M. noto-coxalis tertius* (*16*) and then, more laterally, innervates *M. noto-coxalis secundus* (*15*). These two muscles move the leg posteriorly. In one specimen a branch of the nerve to *M. noto-coxalis secundus*

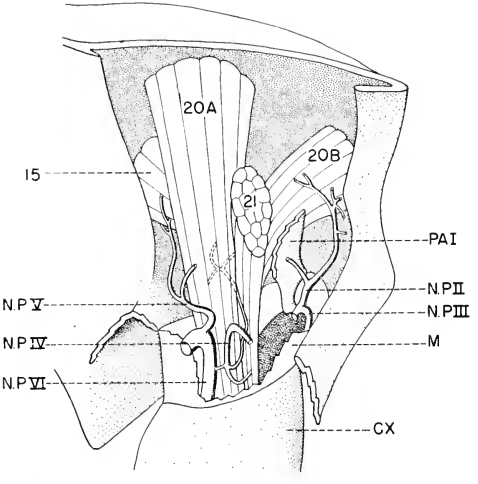

Fig. 9. Medial view of the left half of the prothorax (same view as Fig. 8), with the head removed. The common base of *N.PII*, *N.PIII*, and *N.PIV* has been cut away, leaving *N.PIV* separate from *N.PII* and *N.PIII*. The sternum and furca, and the medial part of the pericoxal membrane have been removed to show the course of *N.PIV*. Muscles *10A*, *10B*, *14*, *16*, and *17*, and the dorsal part of the pleural apophysis have been removed.

appeared to run anteriorly to innervate *M. noto-trochanteralis primus.*

Nervus prothoracicus sextus (*N. PVI*) is the largest of the prothoracic nerves. It passes into the posteromedial part of the coxa and, in the proximal region of the latter, sends off two fairly fine branches which arise at approximately the same level (Fig. 10). One of these goes medially to the intrinsic depressor muscle of the trochanter, *M. coxa-trochanteralis medialis* (*23*; removed in Fig. 10) while the other extends posterolaterally to innervate the posterior and lateral bundles of *M. coxa-trochanteralis lateralis* (24). Near the distal end of the coxa it is joined by one of the two branches of *nervus prothoracicus tertius.* It then passes into the trochanter and runs to the end of the leg, innervating the other intrinsic muscles.

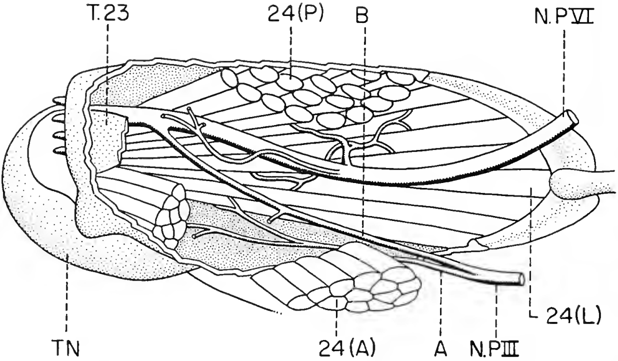

Fig. 10. Medial view of the left prothoracic coxa, with the medial wall cut away. Muscle *23* has been removed, and Tendon *23* has been cut off at the base. The anterior bundle of Muscle *24* is displaced and its middle part is omitted.

Posterior Ganglion. The posterior ganglion (''mid-thoracic ganglion'' of Hamilton, 1931; ''pterothoracic ganglionic center'' of Malouf, 1933; ''Bauch-ganglion'' of Graichen, 1936; ''thoraco-abdominal ganglion'' of Rawat, 1939; ''last ganglion'' of Johansson, 1957; ''pterothoracic-cum-abdominal ganglion'' of Akbar, 1958) is larger and more elongate than the prothoracic ganglion (Fig. 1). It represents the fused mesothoracic, metathoracic, and abdominal ganglia, and gives rise to three groups of nerves. The mesothoracic nerves pass anterior to the mesothoracic furcae, and the metathoracic nerves run between the mesothoracic and metathoracic furcae, while the abdominal nerves lie medial to the latter.

Mesothoracic Nerves (Figs. 11, 12, 13)

Nervus mesothoracicus primus (*N.MI*) ("nerve d" of Malouf, 1933, and Akbar, 1958; "first mesothoracic nerve" of Johansson, 1957) arises from the anterolateral part of the posterior ganglion (Fig. 1). Its base passes ventral to *M. mesosterni primus* (*32*), which depresses the prothorax (Figs. 11, 13). In the mesothorax this ventral longitudinal muscle is innervated by a very short, fine nerve coming off from the posterior ganglion just at the base of *nervus mesothoracicus primus;* this may be interpreted either as two nerves arising simultaneously or as a single nerve branching immediately. In the prothorax, as has been mentioned, the corresponding ventral longitudinal muscles (*Mm. prosterni primus et secundus*) are innervated by a branch of the first prothoracic nerve.

After turning dorsally, *nervus mesothoracicus primus* divides into three main branches (Figs. 11, 13). One of these, *nervus capitis-mesothoracicus* (*N.CM*), has already been discussed; it passes anteriorly through the prothorax and into the head, innervating *M. dorsoventralis* (*9*) and joining *nervus prothoracicus primus*. A second branch, the thickest of the three, passes anterior to *M. dorsoventralis primus* (*34*) and runs anterolaterally, just inside of and parallel to the prealar membrane of the mesothorax (Fig. 11). It corresponds to "branch y of nerve d," as described by Malouf (1933). Laterally, it bifurcates, forming a fine nerve which sends rami to the region of the prealar membrane and a thicker nerve which runs into the base of the wing in the region of the third axillary sclerite (*AXII*; Fig. 13). The third branch of *nervus mesothoracicus primus* extends dorsally and branches extensively, as shown in Figure 11. The rami are quite fine and difficult to trace in dissections, and it is quite probable that there is some individual variation in their arrangement. One nerve from the ventral part of this third branch runs posteriorly and then laterally to innervate the mesothoracic scolopophorous organ (to be described in a later paper). Another ramus extends posteriorly to innervate the more lateral of the two dorsal longitudinal indirect flight muscles, *M. mesonoti secundus* (*31*). The third branch of *nervus mesothoracicus primus* also sends two main rami to the more medial dorsal longitudinal indirect flight muscle, *M. mesonoti primus* (*30*). The nerve to *M. mesonoti secundus* usually appears as a branch of the thicker and more posterior of these two rami. From the thinner, more anterior ramus, a fine nerve runs anteriorly, to the region of the parapsidal membrane.

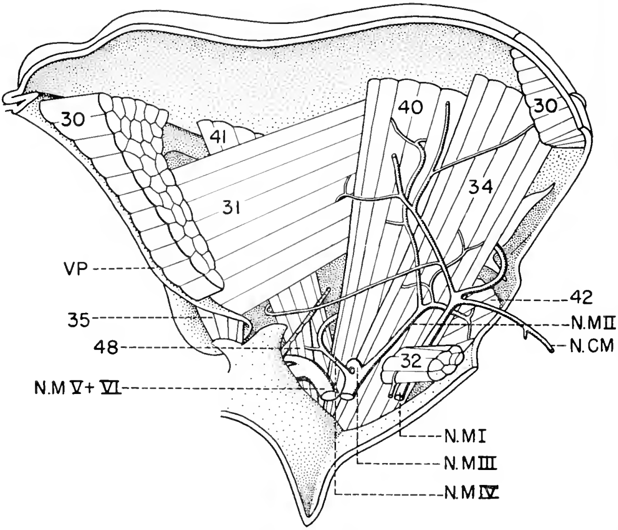

Fig. 11. Medial view of the left half of the mesothorax, showing the innervation of the more medial muscles. The middle part of Muscle *30* and the origin and insertion of Muscle *32* are omitted, and the lateral part of the furcal apodeme has been cut off.

These branches of *nervus mesothoracicus primus* which innervate the dorsal longitudinal indirect flight muscles are quite fine, especially the ramus to the more lateral muscle. In most *Gelastocoris* these muscles, along with the dorsoventral indirect flight muscle, *M. dorsoventralis primus* (*34*), are degenerate (Parsons, 1960), although they appear well developed in some individuals. In the present study, specimens of each type were examined, and the nerves to these flight muscles appeared to be equally fine regardless of the condition of the muscles.

Nervi mesothoracici secundus, tertius, et quartus arise together from the posterior ganglion (Fig. 1), their common base corresponding to "nerve e" of Malouf (1933) and the "second

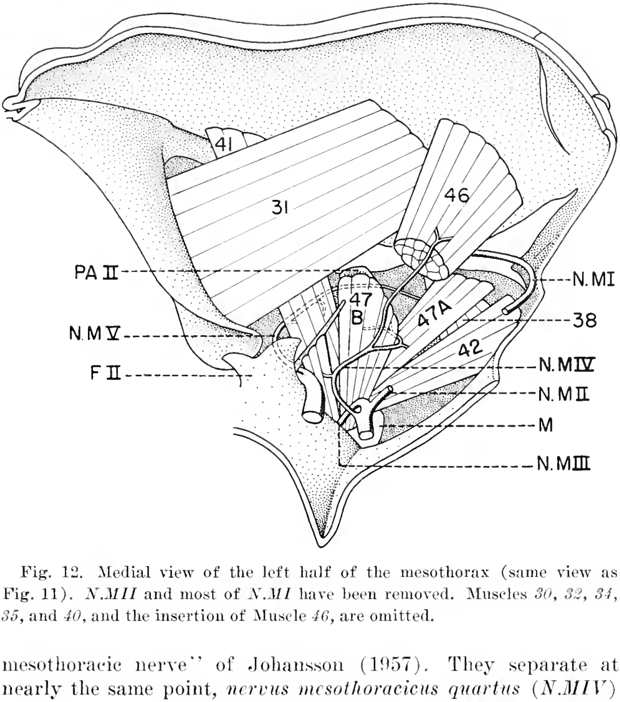

Fig. 12. Medial view of the left half of the mesothorax (same view as Fig. 11). *N.MII* and most of *N.MI* have been removed. Muscles *30, 32, 34, 35,* and *40,* and the insertion of Muscle *46,* are omitted.

mesothoracic nerve" of Johansson (1957). They separate at nearly the same point, *nervus mesothoracicus quartus* (*N.MIV*) branching off slightly before the other two. *Nervus mesothoracicus secundus* (*N.MII*) extends anterodorsally (Fig. 11) and bifurcates just medial to *M. dorsoventralis primus* (*34*). One branch runs posterodorsally to innervate one of the promotor muscles of the leg, *M. noto-trochantinalis* (*40*), while the other passes anteriorly to supply the pleural promotor muscle of the leg, *M. episterno-coxalis* (*42*). From this second branch, very near to the point of bifurcation, a fine nerve runs directly to the dorsoventral indirect flight muscle, *M. dorsoventralis primus* (*34*).

Nervus mesothoracicus tertius (*N.MIII*) goes between *M. dorsoventralis primus* (*34*) and *M. noto-trochantinalis* (*40*), and, like the corresponding nerve of the prothorax, passes into the anteromedial part of the coxa (Figs. 12, 13). Within the coxa it divides, the two branches innervating the anterior and lateral bundles of *M. coxa-trochanteralis lateralis*, as in the prothoracic leg. Similarly, one branch joins *nervus mesothoracicus sextus*

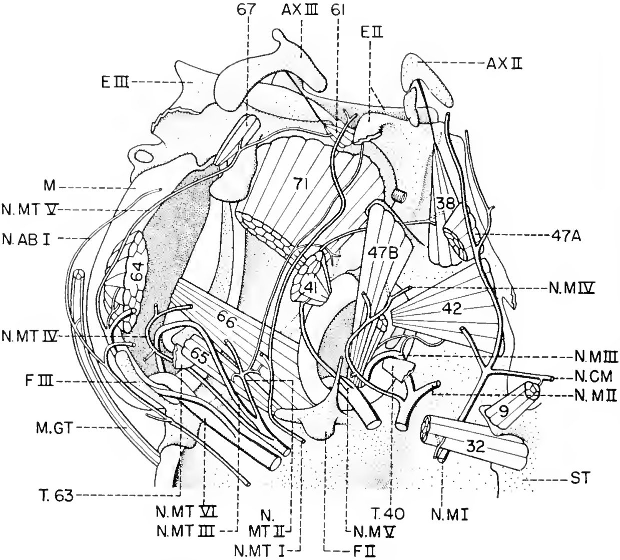

Fig. 13. Dorsal view of the inner surface of the pterothorax, left side, showing the innervation of the ventral and lateral muscles. The posterior part of the prosternum is shown in place. The dorsal parts of the mesothoracic and metathoracic nerves have been cut off. The insertion of Muscle *71* and the origins of Muscles *9*, *32*, *41*, *64*, and *M.GT*, along with the middle part of Muscle *47A*, are omitted. Muscles *40*, *48*, *63*, and *72* have been removed, and Tendons *40* and *63* are cut off near their bases.

at the distal end of the coxa. Before entering the coxa, *nervus mesothoracicus tertius* gives off a very fine branch which soon divides, sending one nerve anteriorly and one posteriorly (Fig. 13). The anterior nerve runs to the mesothoracic episternum and branches extensively along the inner surface of the latter, ventral to *M. episterno-coxalis* (*42*). The posterior nerve extends into the coxal cavity and sends off minute branches along the pericoxal membrane and basicostal ridge, in the region of the mesothoracic trochantin.

Nervus mesothoracicus quartus (*N.MIV*) is more slender than the two preceding nerves. It runs medial and posterior to *M. noto-trochantinalis* (*40*), sending off a short process to one of the extrinsic depressor muscles of the trochanter, *M. furca-trochanteralis* (*48*) (Figs. 11, 12). It then passes dorsolaterally and divides to innervate the other extrinsic depressor muscles of the trochanter (Figs. 12, 13). One branch goes dorsally to *M. noto-trochanteralis* (*46*) while the other supplies *Mm. pleura-trochanterales primus* (*47A*) *et secundus* (*47B*).

Nervi mesothoracici quintus et sextus have a common base (Fig. 1) which corresponds to ''nerve f'' of Malouf (1933), ''nerve 5'' of Rawat (1939) and the ''third mesothoracic nerve'' of Johansson (1957). *Nervus mesothoracicus quintus* (*N.MV*) passes beneath the furcal apodeme, between the mesothoracic furca (*FII*) and *M. furca-trochanteralis* (*48*), and extends posterolaterally around *M. noto-coxalis* (*41*), the remotor muscle of the leg (Figs. 12, 13). After sending off two branches to the latter, it runs laterally and anteriorly, its diameter becoming somewhat decreased. Passing lateral to the pleural apophysis, it innervates the flexor muscle of the forewing, *M. episterno-alaris* (*38*), in the region of the mesothoracic episternum (Fig. 13).

The large *nervus mesothoracicus sextus* (*N.MVI*) runs directly into the posteromedial part of the coxa and, like *nervus prothoracicus sextus*, sends off one branch to the intrinsic depressor muscle of the trochanter (*M. coxa-trochanteralis medialis*) and a second to the posterior and lateral bundles of the trochanteral levator muscle (*M. coxa-trochanteralis lateralis*). It is joined by a branch from *nervus mesothoracicus tertius* in the distal part of the coxa; from here it passes on through the mesothoracic leg and, like *nervus prothoracicus sextus*, innervates the other intrinsic leg muscles.

Metathoracic Nerves (Figs. 13, 14, 15, 16)

Nervus metathoracicus primus (*N.MTI*), which represents "nerve g" of Malouf (1933) and the "first metathoracic nerve" of Johansson (1957), is quite narrow. It curves around the anterior edge of the mesothoracic furca and then bifurcates. One branch continues to run laterally, along the dorsal surface of *M. pleura-trochanteralis* (*71*; Figs. 13, 15). Near the origin of this muscle it turns posterolaterally, passing between *M. pleura-trochanteralis* and *M. noto-trochanteralis* (*70*; Fig. 14)

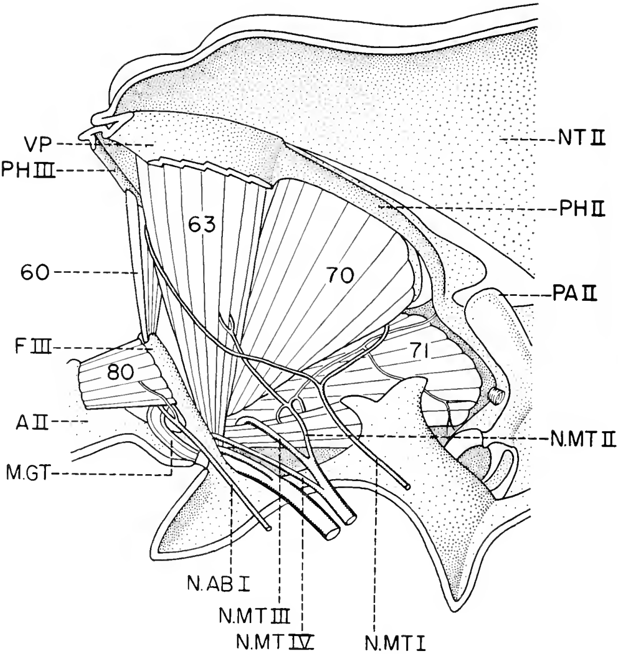

Fig. 14. Medial view of the left half of the metathorax, showing the innervation of the more medial muscles. The ventral process of the mesothoracic phragma has been cut off.

and finally branching into a fine network in the region of the membrane at the base of the hindwing, dorsal to *M. episterno-alaris* (*61*). The second branch of *nervus metathoracicus primus* extends posterodorsally, medial to *M. noto-trochantinalis* (*63*), and then passes laterally between that muscle and *M. dorsoventralis* (*60*; Figs. 14, 15, 16). Here it divides into two slender nerves, one of which goes directly dorsally to the posteromedial region of the metanotum; the other nerve runs between *M. dorso-ventralis* and *M. noto-coxalis* (*64*), and sends branches to the posterolateral region of the metanotum and to the metathoracic scolopophorous organ.

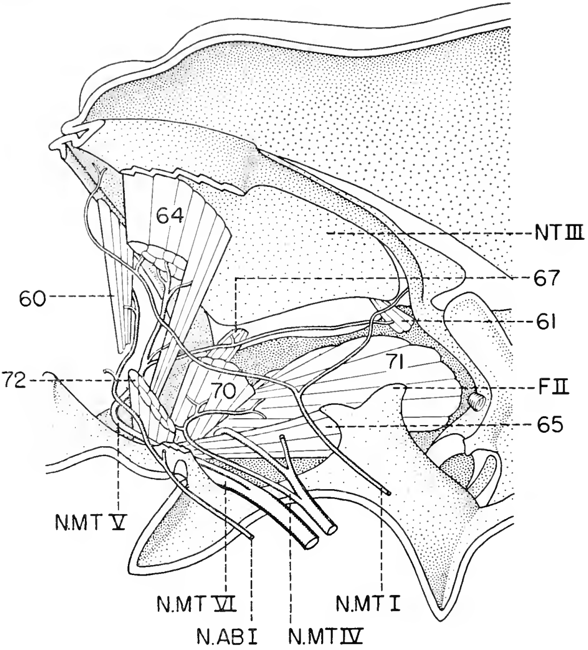

Fig. 15. Medial view of the left half of the metathorax (same view as Fig. 14). *N.MT II*, the metathoracic furca, Muscles *63, 80*, and *M.GT*, and part of Muscles *64* and *70* have been removed.

Nervi metathoracici secundus, tertius, et quartus have a common base, probably corresponding to "nerve h" of Malouf (1933). The slender *nervus metathoracicus quartus* separates from the other two before the latter diverge. *Nervus metathoracicus secundus* (*N.MTII*) goes posterolaterally and dorsally to innervate the promotor muscle of the leg, *M. noto-trochantinalis* (*63*; Fig. 14). Before turning dorsally, it gives rise to two fine branches which extend ventrally, one supplying *M. furca-trochantinalis* (*65*) and the other *M. episterno-coxalis* (*66*; Fig. 13). These two muscles also promote the hindleg. A long and very fine branch from the nerve to *M. episterno-coxalis* runs laterally along the dorsal surface of *M. pleura-trochanteralis* (*71*), parallel to the lateral branch of *nervus metathoracicus primus*. In the area just posterior to the mesothoracic *M. noto-coxalis* (*41*) it appears to divide; one ramus goes laterally and branches extensively in the region where the mesothoracic phragma (*PHII*) joins the pleuron, while the other ramus extends anteriorly, sending many fine branches to the pleuron at the boundary between the mesothorax and metathorax (Figs. 13, 14). These two rami are very slender and difficult to trace.

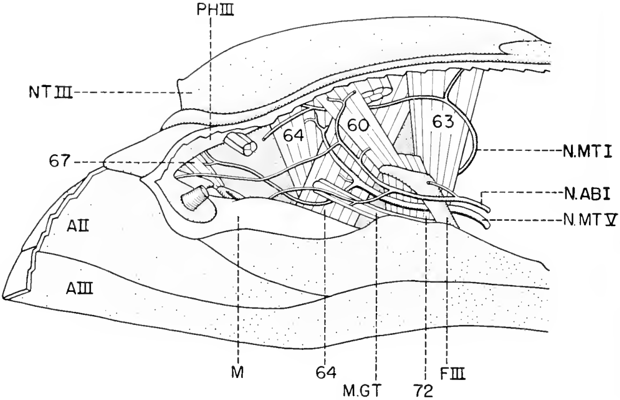

Fig. 16. Posterior view of the left half of the metathorax, showing the innervation of the posterior metathoracic muscles. The terga of the first three abdominal segments have been removed. The abdominal muscles and part of Muscles *60* and *M.GT* are omitted.

Nervus metathoracicus tertius (*N.MTIII*) goes posteriorly and, passing lateral to *M. noto-trochantinalis* (*63*), enters the anteromedial portion of the coxa (Fig. 13). There, like the third prothoracic and mesothoracic nerves, it bifurcates, innervates the anterior and lateral bundles of *M. coxa-trochanteralis lateralis*, and finally joins *nervus metathoracicus sextus*. Its general appearance is similar to that of *nervus prothoracicus tertius*, as shown in Figure 10.

The slender *nervus metathoracicus quartus* (*N.MTIV*) runs posteriorly and passes between *M. noto-trochantinalis* (*63*) and *M. furca-trochanteralis* (*72*). It gives off a short branch to the latter, one of the extrinsic depressor muscles of the trochanter, and then goes laterally to innervate the two larger extrinsic trochanteral depressor muscles. One of its branches extends dorsally to supply *M. noto-trochanteralis* (*70*) and another laterally to *M. pleura-trochanteralis* (*71*; Fig. 15). *Nervus metathoracicus quartus* probably represents "nerve 6a, branch IV" of Rawat (1939).

The common base of *nervi metathoracici quintus et sextus* corresponds to "nerve i" of Malouf (1933) and "nerve 6b" of Rawat (1939). The smaller of these two nerves, *nervus metathoracicus quintus* (*N.MTV*) (the "fine branch of nerve 6b" mentioned by Rawat, 1939), goes posteriorly between the metathoracic furca (*FIII*) and *M. furca-trochanteralis* (*72*), and then curves around the latter muscle in a dorsolateral direction (Figs. 13, 15, 16). Just lateral to the tip of the furca it divides into a large dorsal branch, a more slender ventral one, and a short middle branch. The dorsal and middle branches supply the remotor muscle of the hindleg, *M. noto-coxalis* (*64*), which consists of two bundles, as shown in Figure 16. The ventral branch of *nervus metathoracicus quintus* goes laterally around the base of *M. noto-coxalis* and then turns anteriorly into the lateral part of the metathorax (Figs. 13, 15, 16). Here it sends a short branch to *M. coxa-subalaris* (*67*) and then continues forward as a very fine nerve to *M. episterno-alaris* (*61*), which flexes the hindwing. Both of these are direct flight muscles, the former inserting on the subalare and the latter on the third axillary sclerite of the metathorax (*AXIII*).

The large *nervus metathoracicus sextus* (*N.MTVI*) resembles *nervus prothoracicus sextus* and *nervus mesothoracicus sextus* in its branching and in the muscles which it innervates. It enters the posteromedial part of the metathoracic coxa and sends branches to *M. coxa-trochanteralis medialis* and to the posterior and lateral bundles of *M. coxa-trochanteralis lateralis.* Then, joined by a branch of *nervus metathoracicus tertius*, it continues through the hindleg, innervating the intrinsic muscles.

Abdominal Nerves (Figs. 1, 13, 14, 15, 16, 17)

Since the anatomy of the abdomen of *Gelastocoris* has not yet been described, the abdominal nerves were not studied in any great detail. The following account is only general, and a more inclusive description must await a future study of the musculature, of the internal organs, and, especially, of the genitalia. The abdomen is supplied by five pairs of nerves, *nervi abdominales primus* through *quintus* (Figs. 1, 17). The first four of these are quite fine, while the fifth and most medial nerve is quite stout.

Nervus abdominalis primus (*N.ABI*), which comes off from the posterior ganglion anterior to and somewhat apart from the other four abdominal nerves (Fig. 1), innervates both metathoracic and abdominal muscles. Malouf (1933) and Johansson (1957) have described a similar function for the "first abdominal nerve" of *Nezara* and *Oncopeltus*, respectively. In *Gelastocoris* this nerve extends posterior to the base of the metathoracic furca and sends off a fine branch dorsally to supply *M. ventralis abdominalis* (*80*; Figs. 14, 17). The main body of the nerve passes ventral to that muscle and goes parallel and somewhat dorsal to *nervus metathoracicus quintus* (Fig. 16). Also running parallel to these two nerves is a very long and slender muscle, *M. glandulae thoracicae* (*M.GT*), which was not described in my previous paper on the thoracic musculature (Parsons, 1960). This muscle inserts on the opening of the metathoracic scent gland, in the region of the metathoracic furca (*FIII*), and originates on the lateral part of the metathoracic phragma (*PHIII*) (Figs. 13, 16). In the region behind the metathoracic furca, *nervus abdominalis primus* sends a branch ventrally (Figs. 13, 16); this branch, corresponding to "branch q of the first abdominal nerve" of Malouf (1933), lies along the dorsal surface of *M. glandulae thoracicae* for some distance, and appears to send a short ramus to innervate it (this could not be determined in the dissections but was observed histologically). After the muscle turns dorsally, the ventral branch of *nervus abdominalis primus* runs laterally to the posterior part of the metathoracic pericoxal membrane (*M*) and innervates the scolopophorous organs of the first abdominal segment.

After sending off this ventral branch, *nervus abdominalis primus* extends dorsolaterally, sending a branch to the dorsoventral metathoracic muscle, *M. dorsoventralis* (*60*; Fig. 16). It then runs dorsally and innervates the tergal longitudinal muscles of the reduced first abdominal segment. Between this point and the branching off of the nerve to *M. dorsoventralis*, a long, fine ramus is given off which runs laterally to supply

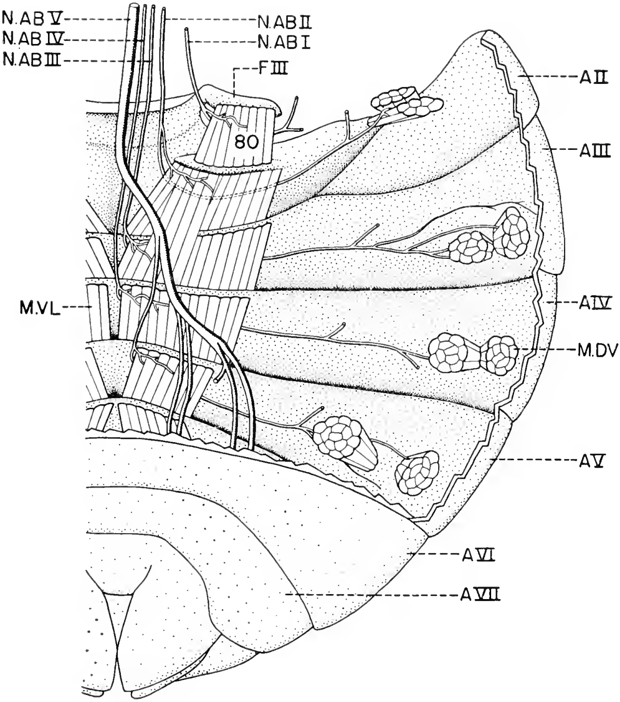

Fig. 17. Dorsal view of the inner surface of the abdomen, right side, showing the innervation of the ventral longitudinal and the dorsoventral abdominal muscles. The terga of the first five abdominal segments, and the tergal longitudinal muscles, are omitted. Only the right-hand nerve of each pair of abdominal nerves is shown.

the membrane at the base of the hindwing, in the region of the subalare and *M. coxa-subalaris* (*67*; Fig. 16). In one specimen it appeared to send a branch to the latter muscle, but in the rest of the dissections that muscle seemed to be innervated only by *nervus metathoracicus quintus.*

Nervi abdominales secundus, tertius, et quartus (*N.ABII-IV*) come off very close together from the caudal part of the posterior ganglion, just lateral to *nervus abdominalis quintus* (*N.ABV*; Fig. 1). They innervate the second, third, and fourth abdominal segments, respectively (Fig. 17). Each nerve bifurcates just medial to the ventral longitudinal muscles (*M.VL*) of its particular segment, one branch innervating those muscles dorsally and the other passing ventral to them. The latter nerve runs laterally and branches extensively, sending fine rami to the dorsoventral (*M.DV*) and dorsal longitudinal muscles of the segment.

The fifth abdominal segment and all segments posterior to it are supplied by branches of the median *nervus abdominalis quintus* (''ventral nerve cord'' of Hamilton, 1931, and Akbar, 1958; ''median nerve'' of Malouf, 1933; ''genital nerve'' of many authors) (Fig. 17). The branching of this large, paired nerve shows considerable individual variation. It innervates the gut and the reproductive organs as well as the musculature of the terminal abdominal segments. Its size and the fact that it supplies several segments indicate that *nervus abdominalis quintus* represents several abdominal nerves which have become fused.

Among the Heteroptera the degree of fusion of the abdominal nerves appears to vary, and the number of separate nerves therefore differs from one group to the next. *Oncopeltus* shows less fusion of the abdominal nerves than most Heteroptera; Johansson (1957) distinguished seven pairs of abdominal nerves in that insect. *Leptocorisa* (Akbar, 1958) and *Nezara* (Malouf, 1933) resemble *Gelastocoris*; both possess five pairs of abdominal nerves, the first four going to the first four segments and the last innervating the following segments. In *Nezara* the two median nerves are fused anteriorly (Malouf, 1933). Pflugfelder's (1936-37) figures show only three pairs of abdominal nerves in *Pentatoma*, *Lethocerus*, and *Notonecta*. In *Nepa*, only the pair of nerves to the first abdominal segment is separate; the rest are fused into the median ''ventral nerve cords,'' with the nerves to the second segment coming off near the base of the latter (Hamilton, 1931). *Hydrometra* (Sprague, 1956) and *Naucoris* (Rawat, 1939) also possess only two pairs of abdominal nerves. In the latter insect the first pair innervates the first three segments while the larger second pair supplies the rest of the abdomen.

HISTOLOGY

BRAIN: PROTOCEREBRUM

A. *Optic lobes* (Figs. 18A, 18B)

The optic lobes contain three ganglionic centers, a distal *lamina ganglionaris* (Graichen, 1936; Johansson, 1957; "I optische Ganglion" of Pflugfelder, 1936-37), a median *medulla externa* (Graichen, 1936; Johansson, 1957; "II optische Ganglion" of Pflugfelder, 1936-37), and a proximal *medulla interna* (Graichen, 1936; Johansson, 1957; "III optische Ganglion" of Pflugfelder, 1936-37). The *lamina ganglionaris* (*LG*) is lens-shaped, its convex side facing the retina. It consists of a distal and a proximal layer. The former stains very deeply and has a distinct palisade structure. Sections passing at right angles through this area show it to have a sieve-like appearance; this is in agreement with the observations of Graichen (1936), Pflugfelder (1936-37), and Johansson (1957). The palisade appearance is caused, according to Pflugfelder (1936-37), by the fibers of the optic nerves (*N.OP*) which run to the retina. In the inner layer, which stains more lightly, parallel fibers may be observed running into the outer layer, but the general appearance is less columnar than in the latter.

According to Pflugfelder (1936-37), a two-layered condition of the *lamina ganglionaris* is a characteristic of the totally aquatic bugs (Cryptocerata), the terrestrial and semi-aquatic heteropterans (Gymnocerata) showing only one layer. He described, for *Notonecta* (Cryptocerata), a dark-staining external lamella and an internal light-staining one, the two being sharply separated. Comparison of sections through the *lamina ganglionaris* of *Gelastocoris* with similar preparations of *Notonecta* reveals that the two layers are similar in appearance in the two species, but that the boundary between them is much less clear in *Gelastocoris* than in *Notonecta*. Graichen (1936) distinguished two layers in the *lamina ganglionaris* of *Nepa* (Cryptocerata), an outer "Markpfeiler" and an inner region of loose neuropile. Johansson (1957) observed that the outer region of this ganglion is palisade-like in the gymnocerate *Oncopeltus*, but that there is no stratification of the ganglion.

Many fibers pass between the *lamina ganglionaris* and the *medulla externa* (*ME*) forming the *chiasma externum* (*CE*)

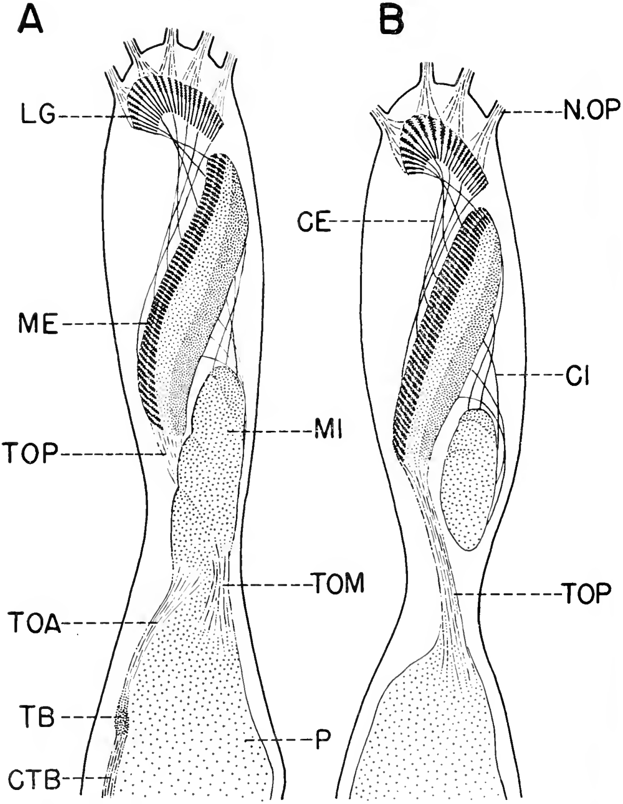

Fig. 18. Frontal sections through the optic lobe of an adult gelastocorid. Figure 18A is taken a few sections dorsal to Figure 18B. Neuropile is stippled; regions of ganglion cells are unstippled. 125 X.

(Graichen, 1936; Johansson, 1957; "äussere Chiasma" of Pflugfelder, 1936-37). These fibers cross over each other in a rather complicated pattern (Figs. 18A, 18B). The *medulla externa*, which is roughly ovoid in shape, is the largest of the three ganglionic centers. It consists of three main strata, a distal one with a columnar structure and two proximal ones with a more homogeneous appearance, lacking striations. In many preparations the outer layer is divided into two by a narrow, light band. It is quite probable that these main lamellae may be even further subdivided; other workers (Graichen, 1936; Pflugfelder, 1936-37; Johansson, 1957) have observed up to 10 layers in the *medulla externa* of various Heteroptera. Graichen (1936) described 6 or 7 strata as the usual condition in *Nepa*, the outermost ones staining most deeply. Johansson (1957) noted three main layers in *Oncopeltus*, the most external one possessing "cross striations." Pflugfelder (1936-37) observed three main lamellae in the Gymnocerata and four in the Cryptocerata examined by him. He reported that the two distal layers in the latter group have a palisade structure and thus correspond to the outermost zone of the Gymnocerata, which has a similar appearance. The columnar layer of the *medulla externa* in *Gelastocoris* may very well represent two separate lamellae, the light central band seen in many preparations being the boundary between them. If so, this ganglion, like the *lamina ganglionaris*, shows the cryptocerate rather than the gymnocerate condition, as described by Pflugfelder (1936-37).

Between the *medulla externa* and the *medulla interna* (*MI*) run fibers which cross over each other, forming the *chiasma internum* (*CI*) (Graichen, 1936; Johansson, 1957; "innere Chiasma" of Pflugfelder, 1936-37). The *medulla interna* consists of four parts, arranged proximo-distally, whose boundaries are much less distinct than those of the two distal ganglia. They are most easily seen in sections dorsal to the *tractus opticus posterior* (*TOP;* Fig. 18A) (to be described below). Three parts lie distal to this tract while the fourth is proximal to it. They show no specialized structure except that the most distal region stains more deeply than the others. The appearance of the *medulla interna* in *Gelastocoris* and the arrangement of its zones in relation to the *tractus opticus posterior* are in agreement with the descriptions of Pflugfelder (1936-37), who observed four parts in both the Gymnocerata and the Cryptocerata. Graichen

(1936) and Johansson (1957) described only two regions in the *medulla interna* of *Nepa* and *Oncopeltus,* respectively.

The fibers from the optic lobes run to the main protocerebral lobes in three optic tracts. The *tractus opticus posterior* (*TOP*) (Pflugfelder, 1936-37; Johansson, 1957) extends from the *medulla externa* to the posterior region of the protocerebrum, passing posteroventral to the *medulla interna* (Fig. 18B). The *tractus opticus anterior* (*TOA*) (Pflugfelder, 1936-37; Johansson, 1957) goes from the *medulla interna* to the anterior part of the protocerebrum, where it meets a deep-staining glomerulus which probably represents the *tuberculum opticum* (*TB*) of Pflugfelder (1936-37) and Johansson (1957)(Fig. 18A). This glomerulus lies ventral to the globuli cells of the corpus pedunculatum and lateral to the central body (to be described later), in the region of the base of the ocellar nerve. The *tubercula optica* of the two sides of the brain are united by a commissure (*CTB*) which corresponds to the "vordere Kommissur" of Pflugfelder (1936-37) and "commissure 13" of Johansson (1957). A third group of fibers runs from the *medulla interna* to the protocerebrum, entering the latter between the *tracti optici anterior et posterior.* The fibers appear to enter at several different places, and it is difficult to trace their individual paths. This tract shall here be termed the *tractus opticus medialis* (*TOM;* Fig. 18A); it probably corresponds to the "Tractus opticus medialis superior" plus the "Tractus opticus medialis inferior" of Pflugfelder (1936-37).

B. *Central body* (Figs. 19A, 19B, 19D)

The central body (*CB*) is a large glomerular structure consisting of three parts, a *dorsal body* (*CBD*) (Johansson, 1957; "äussere Schale" of Graichen, 1936), a *ventral body* (*CBV*) (Johansson, 1957; "Mediankörper" of Graichen, 1936), and a pair of posterior *tubercles* (*CBT*) (Johansson, 1957; "Zentralkörperspindeln" of Graichen, 1936; "Knollen" of Pflugfelder, 1936-37). The dorsal body, the largest of the three parts, embraces the ventral body dorsally and laterally. Rawat (1939) appears to have mistaken it for the protocerebral bridge. In transverse sections through the brain it is U-shaped, its arms extending ventrally, while the ventral body appears fan-shaped (Fig. 19B). The two tubercles, which lie on either side of the midline just posterior to the ventral body, were considered by Graichen (1936) to be part of the dorsal body. They are spherical or oval in shape, their long axes extending dorsoventrally (Fig. 19D).

The entire structure is an association center receiving fibers from many parts of the brain; the paths of some of these fiber tracts have been described by Graichen (1936), Pflugfelder (1936-37), and Johansson (1957). A large number of them enter the lightly-staining hilus or median part of the ventral body and run through its deeper-stained peripheral part into the dorsal body. The paths of these radiating fibers separate the dorsal and ventral bodies into 10 wedge-shaped sections. In transverse sections through the brain the outer edge of the ventral body appears scalloped, the scallops corresponding to the 10 sections. Both Graichen (1936) and Johansson (1957) have similarly reported the division of the central body into 10 sections.

C. *Protocerebral bridge* (Figs. 19C, 19D)

The protocerebral bridge (*PB*) (''pons cerebralis'' of many authors; ''Brücke'' of Graichen, 1936) consists of a pair of small, irregularly shaped glomeruli on either side of the midline which are united medially by a short commissure (''commissure 14'' of Johannson, 1957). The structure is bow-shaped, the arms of the bow extending posteriorly. It lies between the ganglion cells and the neuropile of the brain, dorsal and somewhat posterior to the central body, medial to the globuli cells of the corpora pedunculata (*GB*), and somewhat posterior to the pars intercerebralis.

The roots of the ocellar nerves (*N.O*) lie very close to the posterior arms of the protocerebral bridge. These ocellar roots appear to split up into at least two parts in this region. There seems, however, to be no interchange of fibers between the ocellar nerves and the protocerebral bridge. This is in agreement with the observations of Pflugfelder (1936-37). Although many workers on the insect nervous system have believed the protocerebral bridge to be associated with the ocellar nerves, this structure has been found to be well developed in many insects which lack ocelli, such as the totally aquatic bugs (Graichen, 1936; Pflugfelder, 1936-37).

The protocerebral bridge receives fibers from many parts of the brain. In *Gelastocoris*, fibers were observed running to it from the central body, the pars intercerebralis, the *tractus opticus posterior*, and the protocerebral lobes in general. Similar fiber tracts have been observed by Pflugfelder (1936-37) and Johansson (1957).

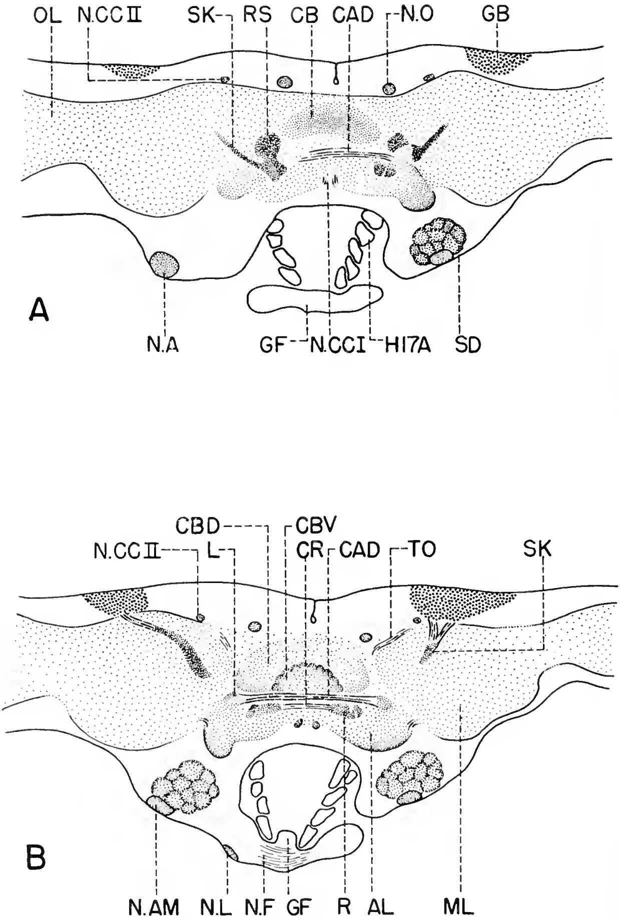

Fig. 19. Transverse sections through the brain of an adult gelastocorid, moving from anterior (Fig. 19A) to posterior (Fig. 19D). Neuropile is stippled; muscles and regions of ganglion cells are unstippled. 120 X.

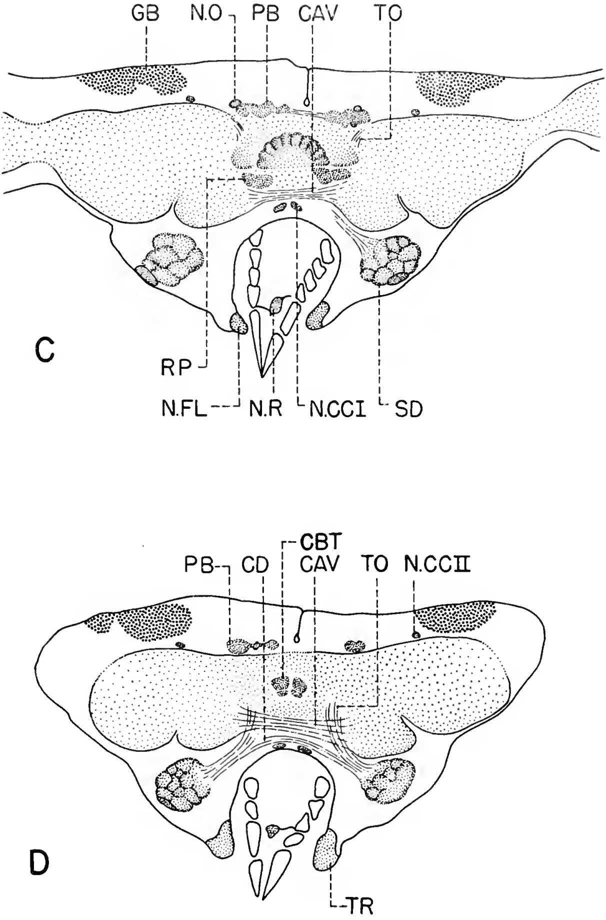

Fig. 19 (continued).

D. *Corpora pedunculata* (Figs. 19A, 19B, 19C)

The corpora pedunculata are paired association centers, each consisting of a large group of *globuli cells* (*GB*) and a stalk (*SK*) which ends in irregularly branched *roots* (*R*). The globuli cells lie just external to the neuropile in the posterodorsal part of the protocerebrum, lateral to the protocerebral bridge. Their nuclei are smaller (5-6 μ) and richer in chromatin than those of the surrounding ganglion cells, and they contain less cytoplasm. They are closely packed, and cell boundaries are difficult to distinguish. Among the globuli cells mitotic figures are quite frequently observed.

The globuli cell mass is roughly circular, its diameter being typically around 120 μ in adult gelastocorids. The cells are organized into two groups, one medial and one lateral; in a few preparations these two groups are somewhat separated, but in most there is no clear boundary between them. The fibers from these two regions, however, emerge as two separate branches, which soon unite to form the common stalk (Fig. 19B) ("Pilzstiel" of Graichen, 1936; "Ramus communis descendens" of Pflugfelder, 1936-37). A second, more weakly developed fiber tract, the *tractus olfactorius* (*TO*) (to be discussed later), runs from the medial part of the globuli cell mass to the deutocerebrum. The medial and lateral groups of globuli cells together correspond to the "oberer Glomerulus" of Pflugfelder (1936-37) and the "dorsal glomerulus" of Johansson (1957). Both these authors also noted the two-part organization of this glomerulus; they also, however, observed a second, smaller glomerulus (the "unterer Glomerulus" of Pflugfelder, 1936-37, and the "ventral glomerulus" of Johansson, 1957) lying ventral to the first and sending fibers to the motor part of the deutocerebrum. No such ventral glomerulus was noted in the present study. Graichen (1936) described only one glomerulus in *Nepa* and did not mention any division into medial and lateral parts. Pflugfelder (1936-37) found the ventral glomerulus to be present in the terrestrial Heteroptera but absent in the semi-aquatic forms which he examined; unfortunately, he did not mention the condition in the totally aquatic bugs.

The stalk of the corpus pedunculatum runs ventromedially and somewhat anteriorly from the globuli cells through the neuropile of the protocerebrum, passing just lateral to the central body. Ventral to the latter, very near the border between the protocerebrum and the deutocerebrum, it branches into several lobes or roots (Figs. 19A-19C) ("Wurzelteil" of Pflugfelder, 1936-37). Two of these roots are very distinct; the *ramus posterior* (*RP;* Fig. 19C) (Johansson, 1957; "innere Wurzel" of Graichen, 1936), which goes posteriorly, ending just ventral to the central body, and the *ramus superior* (*RS;* Fig. 19A) (Pflugfelder, 1936-37; Johansson, 1957; "rückläufige Stiel" of Hanström, 1928, and Graichen, 1936). The latter is the largest of the roots; it extends dorsally and ends lateral to the central body. The roots of the corpora pedunculata of either side are joined by a commissure (*CR;* Fig. 19B) ("Kommissur K_4" of Graichen, 1936). According to Pflugfelder (1936-37) and Johansson (1957) the roots also send fibers to the central body.

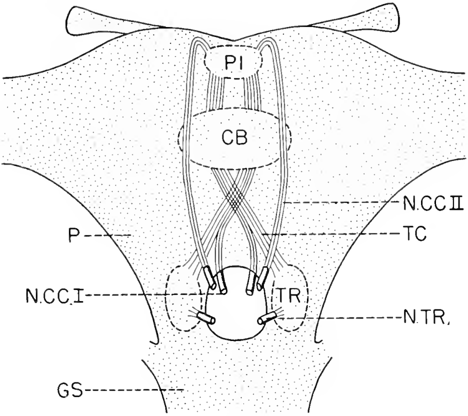

Fig. 20. Diagrammatic dorsal view of the brain, showing the paths of the fiber tracts of *N.CCI*, *N.CCII*, and *N.TR.*

E. *Pars intercerebralis* (Fig. 20)

Beneath the perilemma of the dorsomedial part of the brain lies a group of cells ("Riesenzellen" of Graichen, 1936) which are set off from the ganglion cells by their greater size. These represent the "Pars intercerebralis anterior" of Graichen (1936) and Pflugfelder (1936-37), and the "anterior part of the pars intercerebralis'' of Johansson (1957); they lie anterior to the protocerebral bridge and the central body and anteromedial to the globuli cells of the corpora pedunculata.

Although no special techniques were used to distinguish different cell types in this region, at least two kinds of cells could be observed. Both types are unipolar, sending their processes ventrally into the neuropile of the brain. The first type has much light-staining (gray or light blue in Mallory's triple connective-tissue stain) cytoplasm and a large nucleus which is approximately 15 µ in diameter. The nucleus is spherical or slightly ovoid and typically contains two nucleoli; its chromatin granules are smaller and more dispersed than those of the ganglion cells. Although the exact number of these cells is hard to determine, there appear to be four of them, two on each side of the midline. They lie very close to the midline, and perhaps correspond to the ''D'' cells of Johansson (1958).

The second type of cell is more numerous, there being 8 to 12 of them on either side of the midline. These cells lie lateral to the first type. Their cytoplasm, which stains pink in Mallory's triple connective-tissue stain, is less copious, more granular and deeper-staining than that of the first type of cell. Their nuclei resemble those of the first type except that they are slightly smaller (9-13 µ). Johansson (1958), using Gomori's aldehyde-fuchsin and chrome-haematoxylin-phloxin, distinguished four different cell types in the anterior pars intercerebralis of *Oncopeltus*, which he termed types ''A,'' ''B,'' ''C,'' and ''D.'' The second type of cell observed in the present study probably corresponds to one of the first three of Johansson's types or to a combination of these three.

Posterior to the protocerebral bridge the cells along the median indentation in the dorsal part of the brain appear slightly different from the surrounding ganglion cells. Their nuclei are oval rather than spherical and are slightly smaller than those of the ganglion cells; in some specimens their cytoplasm also stains slightly deeper. It is difficult to say whether they are merely modified ganglion cells or whether they represent the ''Pars intercerebralis posterior'' of Graichen (1936) and Pflugfelder (1936-37) (''posterior part of the pars intercerebralis'' of Johansson, 1957).

The anterior part of the pars intercerebralis sends off fibers to many different parts of the brain. Only four of these tracts could be traced with certainty in the sectioned material of

Gelastocoris. Two of these upon leaving the brain form the *nervi corporium cardiacorum primus et secundus,* which will be described in the section on the endocrine glands. *Nervus corporis cardiaci primus* (*N.CCI*) passes ventral to the central body and crosses over from one side of the brain to the other, while *nervus corporis cardiaci secundus* (*N.CCII*) runs dorsal to the central body and does not cross over (Fig. 20). Both nerves run to the fibro-glial tissue connecting the corpora cardiaca and the corpus allatum. A third tract, the *tractus chiasmaticus* (*TC*) (Pflugfelder, 1936-37; Johansson, 1957), runs posteriorly, to the anteromedial part of the tritocerebrum. The fibers of this strong tract cross over after leaving the tritocerebrum and run ventral to the central body; they are merged, for much of their length, with the fibers of *nervus corporis cardiaci primus* (Fig. 20). A fourth group of fibers was observed running between the pars intercerebralis and the protocerebral bridge; this has also been mentioned by Graichen (1936). Other fiber tracts extend from the pars intercerebralis of *Gelastocoris,* but their destinations could not be determined. In the literature there are references to tracts between this region and the ocellar nerves (Pflugfelder, 1936-37), the central body (Graichen, 1936; Pflugfelder, 1936-37), the corpora pedunculata (Graichen, 1936), the accessory lobes of the protocerebrum (Graichen, 1936), and the deutocerebrum (Graichen, 1936).

F. *Protocerebral lobes* (Fig. 19B)

The protocerebral lobes consist of the large, dorsal *main lobes* (*ML*) (Johansson, 1957; "Hauptlappen" of Graichen, 1936, and Pflugfelder, 1936-37) and the smaller, ventral *accessory lobes* (*AL*) (Johansson, 1957; "Nebenlappen" of Graichen, 1936, and Pflugfelder, 1936-37). The parts of the protocerebrum which have just been described lie predominantly within the main lobes, although the roots of the corpora pedunculata appear to extend into the accessory lobes. The separation between the main and accessory lobes is evident only anteriorly; posteriorly they merge. An indistinct fiber tract ("V_8" of Graichen, 1936) runs between them in the lateral part of the protocerebrum, and fibers also pass between the accessory lobes and the dorsal part of the central body ("V_9" of Graichen, 1936).

In the accessory lobe, just dorsolateral to the roots of the corpus pedunculatum and ventrolateral to the central body, there is a small, roughly spherical area which stains a little more deeply than the surrounding neuropile (*L;* Fig. 19B). It is difficult to see in many preparations. This may represent the "Lateralkörper" of Graichen (1936). Although that author described it as lying between the main and accessory lobes in *Nepa,* it seems to be a dorsomedial part of the accessory lobe in *Gelastocoris.* Two commissures connect these spherical areas of the two sides of the brain; one commissure runs between the central body and the roots of the corpora pedunculata (Fig. 19B), while the second, which is less distinct, passes ventral to the roots of the corpora pedunculata. If these areas are considered to be "lateral bodies," the dorsal and ventral commissures correspond to the commissures "K_2" and "K_3" of Graichen (1936) respectively. It may be, however, that these are merely parts of the accessory lobes and should not be considered as specialized, distinct bodies; if so, the dorsal and ventral commissures are only parts of the two commissures between the accessory lobes (*CAD* and *CAV*) ("K_5" and "K_6" of Graichen, 1936).

In addition to the commissures between the two *tubercula optica,* the two glomeruli of the protocerebral bridge, and the roots of the two corpora pedunculata, which have already been mentioned, a few others are observed in the protocerebral lobes of *Gelastocoris.* The accessory lobes are connected by a pair of commissures, one (*CAD;* Figs. 19A, 19B) running dorsal to the roots of the corpora pedunculata ("K_5" of Graichen, 1936), and the other (*CAV;* Figs. 19C, 19D), very thick, passing ventral to the roots ("K_6" of Graichen, 1936). At least one commissure, and probably more, joins the main lobes dorsally, between the pars intercerebralis and the protocerebral bridge.

BRAIN: DEUTOCEREBRUM

The deutocerebrum of *Gelastocoris* is much smaller than the protocerebrum. It lies posteroventral to the latter and anterolateral to the tritocerebrum with respect to the body. The literature on the heteropteran nervous system reveals that the deutocerebrum consists of an anterior sensory or "olfactory" part and a posterior motor part, the former being more developed than the latter. The antennal nerve receives fibers from each of these regions.

The sensory deutocerebrum ("lobus olfactorius" of many authors) has a distinctly glomerular histological structure, roughly resembling a bunch of grapes (*SD;* Figs. 19A-D, 21).

The glomeruli ("Riechglomeruli" of Pflugfelder, 1936-37) are of various sizes and stain deeply in formalin-fixed material. Pflugfelder (1936-37) has observed that in the terrestrial Heteroptera the sensory part of the deutocerebrum contains a central fibrous mass which is not distinct in the sensory deutocerebrum of the semi-aquatic or aquatic forms. Johansson (1957) likewise noted a fibrous center in the sensory deutocerebrum of the terrestrial bug *Oncopeltus*. No such central fibrous mass was noted in *Gelastocoris*, however.

The sensory parts of the deutocerebral lobes of the two sides of the brain are joined by the *deutocerebral commissure* (*CD*; Fig. 19D) ("K_7" of Graichen, 1936; "commissure 15" of Johansson, 1957), which passes dorsal to the esophagus and ventral to the ventral commissure of the accessory lobes. From the medial part of the sensory deutocerebrum a tract of fibers (*TO*) runs medially and then dorsally, passing between the central body and the roots of the corpus pedunculatum and extending to the medial part of the globuli cell mass of the latter (Figs. 19B, 19C, 19D). This is the *tractus olfactorius* (Pflugfelder, 1936-37; "olfactory tract" of Johansson, 1957; "Riechstrang" of many authors). In *Gelastocoris* it is rather difficult to see, especially in the dorsal part of the brain. Pflugfelder (1936-37) found it to be much better developed in the Gymnocerata than in the Cryptocerata; Johansson (1957) reported it to be well developed in the gymnocerate *Oncopeltus*. In the literature there are references to other fiber tracts, running from the sensory deutocerebrum to the motor deutocerebrum (Pflugfelder, 1936-37; Johansson, 1957), to the central body (Graichen, 1936; Pflugfelder, 1936-37; Johansson, 1957), and to the pars intercerebralis (Graichen, 1936); none of these could be distinguished with certainty in *Gelastocoris*.

The boundaries of the motor part of the deutocerebrum ("lobus dorsalis" or "Dorsalmasse" of many authors) are very hard to distinguish, and the region appears to be greatly reduced in comparison with the sensory part. Its neuropile, which is not glomerular, merges anteriorly with that of the protocerebrum and sensory deutocerebrum and posteriorly with that of the tritocerebrum. Its general position can best be determined by the point of origin of the motor part of the antennal nerve (*N.AM*; Fig. 21). This nerve divides just as it enters the brain, one branch going directly to the sensory deutocerebrum (*SD*) and the other passing posteriorly, lateral to the sensory region, into the motor deutocerebrum (*MD*). Both Pflugfelder (1936-37) and Johansson (1957) observed two parts to the motor branch of the antennal nerve, but these could not be distinguished in the *Gelastocoris* material.

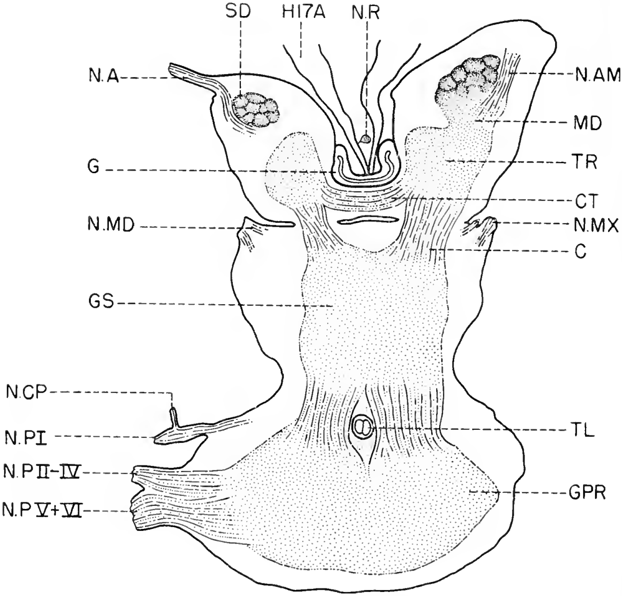

Fig. 21. Frontal section through the deutocerebrum, tritocerebrum, subesophageal ganglion, and prothoracic ganglion of an adult gelastocorid. Neuropile is stippled; muscles, gut, and regions of ganglion cells are unstippled. 120 X.

The reduction of the motor part of the deutocerebrum of *Gelastocoris* may be correlated with the shortness of the antennae. The sensory part appears to be much better developed, and it quite probably supplies antennal sense organs of some sort. Within the antenna the *nervus antennalis* runs through all four segments; since only the basal segment contains muscles (Parsons, 1959), it seems that the distal part of the nerve is chiefly sensory. Graichen (1936) was not able to distinguish a motor deutocerebrum in the totally aquatic bug *Nepa* and believed it to be either degenerate or incorporated into the protocerebrum. She also failed to observe a motor branch to the antennal nerve. Pflugfelder (1936-37) found the deutocerebrum in general to be less developed in the semi-aquatic and totally aquatic Heteroptera than in the terrestrial forms; he proposed that in the totally aquatic bugs this was correlated with the reduced antennae.

BRAIN: TRITOCEREBRUM

The tritocerebrum (*TR;* Figs. 19D, 21) is the least developed part of the brain. It lies posterior to the protocerebrum, posteromedial to the sensory deutocerebrum, and lateral to the gut where the latter passes between the brain and the subesophageal ganglion. Caudally it is joined to the subesophageal ganglion by the short, thick circumesophageal connectives (*C;* Fig. 21). Its neuropile shows no special differentiation.

The tritocerebral region gives rise to two commissures, the small, free *frontal commissure* (*FC;* Figs. 2, 5, 23) and the much larger *tritocerebral commissure* (*CT*), which lies within the main body of the brain (Fig. 21). The fibers of the tritocerebral commissure come off from the tritocerebrum just medial to those of the circumesophageal connectives. The commissure passes beneath the gut (*G*) and lies just anterior to the boundary between the brain and the subesophageal ganglion. It represents the "tritocerebral commissure" of Pflugfelder (1936-37) and Johansson (1957) and the commissure "K_8" of Graichen (1936). Rawat (1939) believed the tritocerebral commissure to be contained within the circumesophageal connectives in *Naucoris;* it was not mentioned by Hamilton (1931) or Titschack (1928).

Of the fiber tracts from the tritocerebrum to other parts of the brain, only the *tractus chiasmaticus* to the pars intercerebralis was clearly seen (*TC;* Fig. 20); this was described earlier. Pflugfelder (1936-37) observed two weaker tracts from the tritocerebrum to the protocerebrum, one entering the latter ventrocaudally and the other laterally.

VENTRAL NERVE CORD

The ventral nerve cord includes the subesophageal, prothoracic, and posterior ganglia. The available histological material did not permit a detailed study of the fine structure of these ganglia, whose neuropile contains a complex system of fiber tracts. The reader is referred to the excellent work of Wigglesworth (1959), who studied the histology of the central nervous system of *Rhodnius* using the osmium/ethyl gallate method.

Graichen (1936) was able to distinguish, in the subesophageal ganglion of *Nepa,* three regions of the neuropile representing the fused "Maxillarganglion," "Mandibularganglion," and "Labialganglion." These she found to be located posterodorsally, anterodorsally, and ventrally, respectively, there being no clear boundaries between them; their position was indicated only by the points of origin of the maxillary, mandibular, and labial nerves. In *Gelastocoris,* these three nerves could be traced for only a short distance in the neuropile. The *nervi mandibulares* (*N.MD;* Fig. 21) enter the latter in the anteriormost part of the subesophageal ganglion, just lateral to the subesophageal connectives. The *nervi maxillares* (*N.MX;* Fig. 21) arise very close to the mandibular nerves; within the neuropile of the ganglion their fibers run somewhat posterior to those of the latter and slightly more ventrad. The maxillary region of the subesophageal ganglion must therefore lie posterior to the mandibular region; this is in agreement with Graichen's (1936) observations, although both of these two regions appear to be located much more anteriorly in *Gelastocoris* than in *Nepa* as indicated by Graichen's Figure 16. The *nervi labiales* arise from the posteroventral part of the subesophageal ganglion, their fibers extending dorsally into the neuropile for a considerable distance. The labial region of the ganglion appears to be located ventral and somewhat posterior to the maxillary and mandibular areas. This agrees, in general, with Graichen's conclusions, although the labial region seems to occupy a more posterior position in *Gelastocoris* than in *Nepa.*

Two short, thick fiber tracts connect the subesophageal ganglion with the prothoracic ganglion (Fig. 21). These represent the two longitudinal connectives between the ganglia, which have become fused medially. Their neurilemmae are separated only at the point where one or two tracheoles (*TL*) run between them dorsoventrally. Graichen (1936) reported the presence, in *Nepa,* of a "Neurilemmstreif" between the subesophageal and prothoracic ganglia, marking the former boundary between them; she did not mention any tracheoles within this band. Most of the fibers of the connectives pass posteriorly through the dorsal and ventral parts of the prothoracic ganglion and continue into the connectives joining the prothoracic and posterior ganglia; a few of the fibers end in the neuropile of the prothoracic ganglion.

The fibers of *nervus prothoracicus primus* (*N.PI*) arise from the anteriormost part of the neuropile of the prothoracic ganglion, just lateral to the connectives. The fibers of the other five prothoracic nerves originate more posteriorly, from many parts of the neuropile; they come together in the lateral part of the ganglion before emerging from it (Fig. 21). Graichen (1936) reported that the prothoracic ganglion of *Nepa* is divided into a dorsal lobe, with loose neuropile, and a ventral, glomerular lobe. No such division was observed, however, in the prothoracic ganglion of *Gelastocoris*.

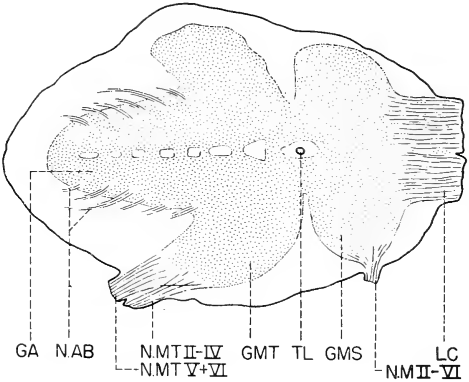

Fig. 22. Frontal section through the posterior ganglion of an adult gelastocorid. Neuropile is stippled; regions of ganglion cells are unstippled. 90 X.

The two longitudinal connectives between the prothoracic and posterior ganglia are entirely separate. They are long and broad, and are flattened for most of their length. The posterior ganglion is very large, and its neuropile is divided into three main regions, representing the fused mesothoracic, metathoracic, and abdominal ganglia (Fig. 22). In the anterior and middle parts of the posterior ganglion lie the lobes of the mesothoracic

(*GMS*) and metathoracic (*GMT*) ganglia. Laterally, these lobes are separated by ganglion cells; medially their neuropile is fused, but the original boundary between them is marked, like that of the subesophageal and prothoracic ganglia, by the path of a small tracheole (*TL*) which penetrates the posterior ganglion dorsoventrally. In some cases this tracheole does not run all the way through the ganglion but penetrates it only dorsally. In these individuals, however, a slender process of the neurilemma surrounding this tracheole continues through the mass of the ganglion to the ventral surface. The first mesothoracic and metathoracic nerves, like the first prothoracic nerve, receive fibers from the anteriormost parts of their respective lobes. The fibers of the posterior five nerves of the mesothorax and metathorax come off from the posterolateral part of the mesothoracic and metathoracic lobes, and arise from many parts of the neuropile.

The neuropile of the fused abdominal ganglia (*GA*) lies posterior and medial to that of the metathoracic ganglion and is continuous with the latter (Fig. 22). The abdominal ganglia consist of two masses of neuropile, which are longer than broad and which are separated by a narrow region of ganglion cells. Between these two masses run at least 8 bands of neuropile and numerous fiber tracts, giving the region a roughly ladder-like appearance. The fibers of the abdominal nerves (*N.AB*) arise from the lateral parts of the two longitudinal masses; most of these fibers run into the two large, medial *nervi abdominales quinti*. The posterior ganglion becomes much flattened and narrowed in its posterior, abdominal region.

STOMODEAL NERVOUS SYSTEM AND ENDOCRINE GLANDS

The stomodeal nervous system consists of the *frontal ganglion*, the *hypocerebral ganglion* (''occipital ganglion'' of many authors; ''posterior sympathetic ganglion'' of Hamilton, 1931), the *nervus procurrens* (''Nervus frontalis'' of Titschack, 1928; ''frontal nerve'' of Malouf, 1933), and the *nervus recurrens*. The frontal ganglion (*GF;* Figs. 3, 5, 19A, 19B, 23), which is connected to the tritocerebrum by the two *nervi frontales*, lies anterior to the brain[1] and dorsal to the gut, between the cibarial and pharyngeal dilator muscles of the food pump. Fibers which

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[1] In the following discussion, the directional terms will be used in relation to the head alone, rather than to the body as a whole.

are continuous with the frontal nerves and the frontal ganglion pass ventral to the gut forming the free *frontal commissure* (*FC;* Figs. 2, 5, 23). From the anterodorsal part of the ganglion the *nervus procurrens* (*N.PR;* Figs. 2, 3, 5, 23) extends forward along the midline, above the food pump; it innervates the cibarial dilator muscles of the pump, *Mm. dilatatores cibarii primus, secundus, tertius, et quartus* (*H14, H15, H16, H17*; Fig. 6).

The *nervus recurrens* (*N.R;* Figs. 3, 19C) runs caudally from the posterior part of the frontal ganglion and passes between the brain and the subesophageal ganglion, dorsal to the gut. The anterior part of the recurrent nerve gives off fine branches to the pharyngeal dilator muscle of the food pump, *M. dilator praepharyngis* (*H17A*; Fig. 6). Just before emerging posterior to the brain, the nerve becomes quite flat and broad, and gives off a very fine lateral branch on either side (Fig. 3); these two branches, as will be described later, join the *nervi corporium cardiacorum primi* from the corpora cardiaca. The flattened, broad part of the recurrent nerve ends as the hypocerebral ganglion (*GH;* Fig. 3) just anterior to the corpus allatum, between the dorsal postpharyngeal dilator muscles. This ganglion does not appear to be associated with either the corpus allatum or the corpora cardiaca. Nabert (1913) observed "Brücken" between it and the corpora cardiaca of *Pyrrhocoris*, and Bickley (1942) has reported the presence of a nerve plexus between the

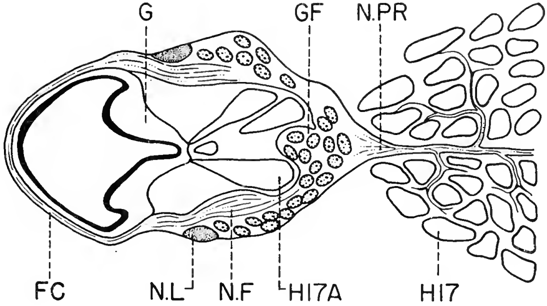

Fig. 23. Transverse section through the gut of an adult gelastocorid, taken at the level of the frontal ganglion, the procurrent nerve, and the frontal commissure. 255 X.

hypocerebral ganglion and the corpora cardiaca in *Nezara* and *Arilus.* Cazal (1948) stated that the hypocerebral ganglion and the corpora cardiaca are in direct contact in the Gymnocerata but not in the Cryptocerata, and that in the Gymnocerata these two bodies probably exchange anastomoses. Akbar (1958) described a "hypocerebral-cum-oesophageal ganglion" in *Leptocorisa;* this apparently consists of the fused hypocerebral ganglion and corpora cardiaca.

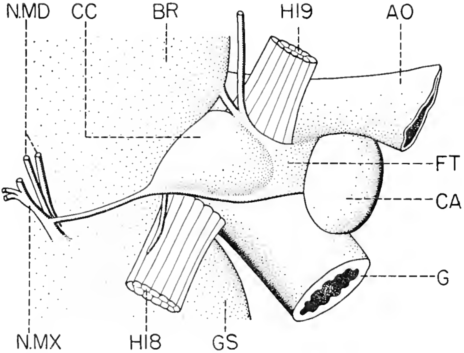

Fig. 24. Lateral view of the corpus allatum and the left corpus cardiacum in an adult gelastocorid, showing the relationship of the glands to the fibro-glial tissue, the gut, the aorta, and the postpharyngeal dilator muscles. The muscles and the maxillary and mandibular nerves have been cut off near their bases.

The hypocerebral ganglion and the two lateral branches of the recurrent nerve were not seen clearly in any of the dissections, and their form and presence were determined only histologically. Some authors (Graichen, 1936; Rawat, 1939; Bickley, 1942; Cazal, 1948; Nayar, 1956a; Akbar, 1958) have described single or paired "esophageal nerves" ("recurrent nerves" of Nayar, 1956a, and Akbar, 1958) running posteriorly from the hypocerebral ganglion in some Heteroptera, but these appear to be absent in *Gelastocoris.*

The endocrine glands consist of the single *corpus allatum* and the two *corpora cardiaca* ("Ganglion pharyngeale" of Nabert, 1913; "lateral sympathetic ganglion" of Hamilton, 1931, and

Graichen, 1936; "oesophageal ganglion" of Rawat, 1939; "corpora paracardiaca" of Cazal, 1948). The corpora cardiaca were mistaken by Malouf (1933) for excretory bodies. The spherical or oval corpus allatum (*CA;* Figs. 1, 4, 24) lies between the esophagus (*G*) and the aorta (*AO*), just posterior to the dorsal postpharyngeal dilator muscles (*H19*). It never appeared to be bilobed, as is the condition in some Heteroptera with single corpora allata (Nabert, 1913, *Gerris*; Johansson, 1957, *Oncopeltus*). Although some asymmetry in the form of this organ seems to be common among the Heteroptera (Nabert, 1913; Bickley, 1942; Cazal, 1948; Johansson, 1957), in the majority of gelastocorids examined it was medial in position rather than displaced to one side (only two of the 7 sectioned adults in which the gland could be clearly seen had displaced corpora allata).

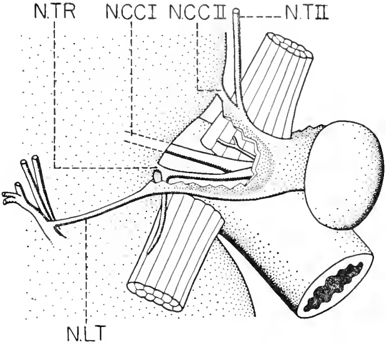

Fig. 25. Same view as Figure 24, with most of the corpus cardiacum cut away to reveal the nerves originating in the fibro-glial tissue.

Among the Heteroptera, single corpora allata are more common than paired ones, the latter condition apparently being confined to the Cryptocerata (Nabert, 1913; Pflugfelder, 1936-37; Hanström, 1941; Cazal, 1948; Benwitz, 1956). Akbar (1958) referred to a "pair" of corpora allata in the terrestrial bug *Leptocorisa* (Coreidae); it seems likely, however, that he was merely implying a bilobed rather than a separated condition. Cazal (1948) found the organ to be unpaired in the coreid *Syromastes.*

The size of the corpus allatum of *Gelastocoris* shows considerable individual variation. In the 7 sectioned adults in which it was distinct, the approximate diameter of the gland ranged from 75 μ to 100 μ. It is composed of closely packed cells with roughly spherical nuclei whose diameter ranges from three to six μ (Fig. 26). These nuclei stain deeply, being rich in chromatin. The light-staining cytoplasm is sparse and homogeneous; very faint cell membranes could be distinguished in some preparations but not in others. Graichen (1936) noted very faint cell membranes in the corpora allata of *Nepa,* and Pflugfelder (1936-37) observed them in some Geocorisae, although Nayar (1956b) reported a syncytial condition in the corpus allatum of *Iphita.* It may be that the presence or absence of cell membranes in this gland varies with its secretory activity, as Wigglesworth (1934) has reported for *Rhodnius.*

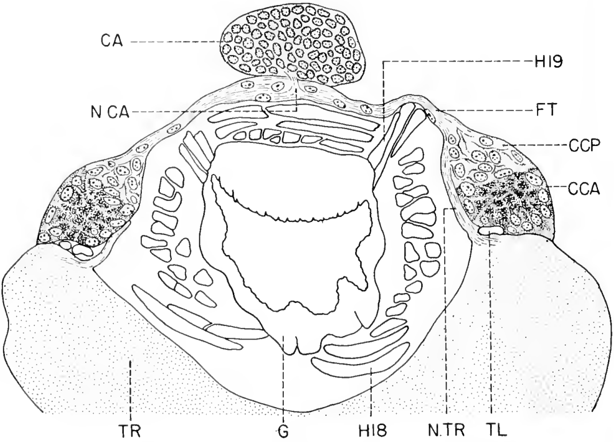

Fig. 26. Transverse section through the brain of a newly-moulted adult *Gelastocoris,* taken at the level of the tritocerebrum, corpus allatum, and corpora cardiaca. The gut and muscles are unstippled. 320 X.

The corpora cardiaca (*CC*) lie on either side of the gut, at the point where the latter emerges from the brain; they are located between the dorsal (*H19*) and ventral (*H18*) postpharyngeal dilator muscles (Fig. 24). These glands are roughly ovoid in form and are generally as large as or slightly smaller than the corpus allatum. The main body of each corpus cardiacum is convex laterally; posteriorly, it is continuous with a flat, broad band of tissue (*FT*) which extends to the corpus allatum (Fig. 24). Some of this tissue also lies along the dorsal and ventral borders of the corpus cardiacum. Histologically, this flattened band resembles nervous tissue (Fig. 26); it represents the "lame fibro-gliale" of Cazal (1948) and the "cardio-glial" tissue of Junqua (1956). Anterior and posterior to the dorsal postpharyngeal dilator muscles, the fibro-glial tissue becomes closely associated with the wall of the aorta, and the two cannot be separated in dissections; histologically, they appear to be continuous with each other. This is in agreement with the observations of other workers on the heteropteran nervous system (Nabert, 1913; Cazal, 1948; Junqua, 1956; Benwitz, 1956, Johansson, 1957).

The fibro-glial tissue extends posteriorly behind the dorsal postpharyngeal dilator muscles and dorsal to the gut, forming a connection ("Pharyngealganglienbrücke" of Nabert, 1913; "Kommissur" of Graichen, 1936) which unites the two corpora cardiaca and the single corpus allatum (Figs. 24, 26). Posterior to each corpus cardiacum the fibro-glial tissue is quite extensive, some of it extending medially to lie between the dorsal muscle and the gland. The boundary between it and the posterior part of the corpus cardiacum is not clear-cut histologically, and the two seem to merge (Fig. 26). All the nerves of the endocrines appear to arise from the fibro-glial tissue where it merges with the posterior part of the gland. Some of the nerve fibers pass into the latter while others run posteriorly in the fibro-glial tissue.

The main mass of the corpus cardiacum is histologically divided into two parts (Fig. 26). Both parts contain cells with spherical or oval nuclei which are larger (4-10 μ) and more variable in size than those of the corpus allatum; they are less closely packed and not as rich in chromatin as the nuclei of the latter gland. In the more anterior part of the corpus cardiacum (*CCA*) (the "vorderen centralen Substanz" of Nabert, 1913), there are very few nerve fibers, and the granular cytoplasm of the cells stains deeply. These represent the "chromophil cells" of Cazal (1948); in some preparations their cytoplasm appears vacuolated. Fairly distinct cell membranes are present. The nuclei appear to be more numerous near the periphery of this anterior portion than in the center; the latter contains mainly dark-staining cytoplasmic processes from the chromophil cells. Cazal (1948) has described a similar peripheral concentration of the nuclei of the chromophil cells in the anterior portion of the corpus cardiacum of *Nepa;* in *Naucoris* and *Notonecta,* however, he found the nuclei to be uniformly distributed throughout this part of the gland.

The posterior portion of the corpus cardiacum (*CCP*) (the "hinteren centralen Substanz" of Nabert, 1913) contains fewer nuclei than the anterior portion. The cytoplasm is granular but lighter staining, and many more nerve fibers are seen running between the cells. These fibers extend into the fibro-glial tissue, which is continuous with this posterior part of the gland. The transition between the anterior and posterior portions of the corpus cardiacum is quite sharp. Both Nabert (1913) and Graichen (1936) reported a layer of ganglionic cells dividing these two regions in *Nepa;* no such layer was observed in *Gelastocoris,* although in 2 out of 11 adults and nymphs examined histologically there appeared to be a very faint septum between the regions.

A histological difference between the anterior and posterior parts of the corpus cardiacum has been described in the totally aquatic bugs *Nepa* (Nabert, 1913; Graichen, 1936; Cazal, 1948), *Naucoris* (Cazal, 1948), *Notonecta* (Cazal, 1948; Nabert, 1913, reported the absence of a separation in this insect, however), *Ranatra* (Cazal, 1948), and *Corixa* (Benwitz, 1956). All these authors mentioned the greater chromophilia in the anterior part and the greater abundance of nerve fibers posteriorly. In *Naucoris* and *Notonecta* there is a visible external constriction between the two parts (Cazal, 1948). Cazal stated that this histological division is a pecularity of the Cryptocerata; he did not describe it in any of the 12 Gymnocerata which he examined. To the author's knowledge, the condition has not been reported in the latter group. The nature and distribution of the fibro-glial tissue form another peculiarity of the Cryptocerata, according to Cazal (1948). He reported that the posterior parts of the two corpora cardiaca of the Gymnocerata fuse directly; the fused portion lacks chromophil cells and corresponds roughly to the fibro-glial tissue but it is not nearly as extensive as that of the Cryptocerata. Cazal also observed that the main mass of the corpora cardiaca in the Gymnocerata is located beneath the aorta, while in the Cryptocerata these glands are mostly independent of the aorta, being separated from it by the dorsal postpharyngeal dilator muscles. In these three respects, *Gelastocoris* resembles the Cryptocerata rather than the Gymnocerata; the corpus cardiacum is histologically divided into two parts and is separated from the aorta by the pharyngeal dilator muscles; also, an extensive and distinct fibro-glial tissue is present. In addition, the general appearance of the corpora cardiaca of *Gelastocoris* bears much more resemblance to those of the Cryptocerata, as figured by Cazal (1948), than to those of the Gymnocerata.

The nerves of the endocrine glands all appear to arise from the fibro-glial tissue at or near its junction with the posterior part of the corpus cardiacum (Fig. 25). From the ventral region of this tissue a slender *nervus lateralis* (*N. LT*) extends anteriorly along the ventral margin of the corpus cardiacum and joins the common base of the maxillary nerves, very close to the place where they enter the subesophageal ganglion. This represents the "ventrale sympathische Nerv" of Graichen (1936), the "posterior lateral nerve" of Cazal (1948), and the "lateral nerve" of Johansson (1957, 1958). Cazal found that this nerve joins the base of the mandibular nerve in the Cryptocerata, but was unable to trace its ending in the Gymnocerata. Johansson reported that it joins one of the maxillary nerves in *Oncopeltus*.

Nervus corporis cardiaci primus (*N.CCI*; Figs. 19A-D, 20, 25) is the most medial of the nerves; since it lies between the corpus cardiacum and the dorsal postpharyngeal dilator muscle it could not be seen with certainty in the dissections, and its course was therefore determined only in sectioned material. It runs from the medial surface of the fibro-glial tissue anteriorly, between the muscle and the gland, and enters the space through which the gut passes between the brain and the subesophageal ganglion (Fig. 25). Here it lies dorsal to the gut and lateral to the recurrent nerve; here also it is joined by the posterior lateral branch from the recurrent nerve which was mentioned previously. Although Pflugfelder (1936-37; many Heteroptera) and Rawat (1939; *Naucoris*) observed no connection between the stomodeal nervous system and the endocrines, both Hamilton (1931; *Nepa*) and Johansson (1957; *Oncopeltus*) reported branches of the recurrent nerve passing directly to the corpora cardiaca. In *Gelastocoris* the connection appears to be indirect, the branches of *nervus recurrens* joining the gland by way of the *nervi corporium cardiacorum primi*. Cazal (1948) stated that "anastomoses endocrino-sympathetiques" are found in the Gymnocerata but not in the Cryptocerata. He may, however, have been referring to the close connection between the hypocerebral ganglion and the corpora cardiaca in the former group and its apparent absence in the latter.

Nervus corporis cardiaci primus enters the medial surface of the brain. Within the latter its fibers merge with those of the *tractus chiasmaticus* (*TC;* Fig. 20). They turn dorsally, cross over to the other side of the brain, and, passing anteroventral to the central body, end in the pars intercerebralis (*PI*). The path of this nerve makes it appear to be homologous with the "nervus corporis cardiaci I" of Hanström (1941) and Johansson (1957, 1958), the "internal paracardial nerve" of Cazal (1948) and Benwitz (1956), and the "cardiac nerve" of Nayar (1956a).

Nervus corporis cardiaci secundus (*N.CCII;* Figs. 19A-D, 20, 25) arises from the dorsal part of the fibro-glial tissue and extends dorsal and lateral to *nervus corporis cardiaci primus.* Running along the dorsal edge of the corpus cardiacum, it enters the brain just anterior to the point where the dorsal dilator muscle (*H19*; Fig. 24) goes medial to the corpus cardiacum. Within the brain it runs dorsally, just external to the neuropile, to the lateral part of the pars intercerebralis, in the region of the ocellar nerve (Fig. 20). *Nervus corporis cardiaci secundus* represents the "nervus corporis cardiaci II" of Hanström (1941) and Johansson (1957, 1958) and the "Nervus paracardialis exterior" of Benwitz (1956). It is probably homologous with the "external paracardial nerve" of Cazal (1948), although it is not, as in the Heteroptera described by that author, fused for much of its length with the "internal paracardial nerve" (*nervus corporis cardiaci primus*).

A third nerve from the brain, the *nervus tritocerebralis* (*N.TR;* Figs. 20, 25, 26), runs ventral and lateral to *nervus corporis cardiaci primus* and enters the ventral part of the fibro-glial tissue. Since it, like the latter nerve, lies medial to the main body of the corpus cardiacum, it was not clearly seen in the dissections, and its course was determined only in sectioned material. The *nervus tritocerebralis* enters the tritocerebrum just medial to the anteroventral border of the corpus cardiacum (Fig. 26). Unfortunately, its course within the brain could not be determined; it appears to go caudally rather than towards the protocerebrum. Shortly before entering the brain it sends a branch ventrally; this branch passes medial to *nervus lateralis* and innervates the ventral postpharyngeal dilator muscle, *M.*

dilator postpharyngis ventralis (*H18*; Fig. 24). Cazal (1948) has described, in *Naucoris*, the innervation of this muscle by a branch of the "internal paracardial nerve" (*nervus corporis cardiaci primus* of the present study), and Benwitz (1956) found it to be innervated, in *Corixa*, by a branch of the combined "paracardial nerves" (*nervi corporium cardiacorum primus et secundus*). It is unlikely, however, that the *nervus tritocerebralis* represents a "paracardial nerve," since the latter enters the protocerebrum rather than the tritocerebrum in other Heteroptera. Johansson has observed a similar and probably homologous "tritocerebral nerve" (1957; "nervus corporis cardiaci III," 1958) in *Oncopeltus*, and suggested that it represents the tritocerebral nerve ("racine tritocérébrale du nerf paracardiaque" of Cazal, 1948) described by Pflugfelder (1936-37) and Cazal (1948) in some Homoptera. Pflugfelder believed the tritocerebral nerve to be absent in the Heteroptera.

Two other nerves run from the fibro-glial tissue to other structures in the head. A very short, fine nerve extends to the dorsal postpharyngeal dilator muscle, *M. dilator postpharyngis dorsalis* (*H19*; Fig. 24); whether this should be considered a separate nerve or a branch of *nervus corporis cardiaci secundus* is unclear, since both nerves break up into small branches in the same region of the fibro-glial tissue. Benwitz (1956) considered this smaller nerve to be a branch of "Nervus paracardialis exterior" (*nervus corporis cardiaci secundus* of the present study) in *Corixa*. A second, much longer nerve, *nervus tegumentarius secundus* (*N. TII*), arises as a definite branch of *nervus corporis cardiacum secundus* (Fig. 25). It runs dorsally, between the dorsal postpharyngeal dilator muscle and the brain, and then extends anterolaterally, lying dorsal to the brain and just lateral to the ocellar nerve (Figs. 3, 5). Here it bifurcates into medial and lateral rami, each of which branches out into the fatty tissue between the brain and the cranial exoskeleton.

The corpus allatum is innervated by at least one, and probably two, *nervi corporium allatorum* (*N.CA*) ("allatic nerve" of Nayar, 1956a and b) from the posteromedial region of the fibro-glial tissue (Fig. 26). This was observed only histologically; it was difficult to determine whether the nerve was single or paired, but one preparation seems to indicate the latter, the two nerves entering the corpus allatum very close together. Cazal (1948) was not able to determine whether or not the "nerf allate" is paired in the Gymnocerata, but he suspected that it is, since he believed the single corpus allatum of this group to have had a paired origin. The probable paired condition of the allatal nerve in *Gelastocoris* supports this theory, which has also been advanced by Nabert (1913) and Pflugfelder (1936-37). The paired nature of the corpora allata of the Cryptocerata is, according to this hypothesis, primitive. Nabert (1913) suggested that the single, symmetrical corpus allatum of the semi-aquatic bug *Gerris* represents a transition between the paired and the often asymmetrical unpaired condition, as seen in the totally aquatic and the terrestrial Heteroptera, respectively.

DISCUSSION

The previous works on the heteropteran nervous system have dealt chiefly with the structure of the brain and with the paths of the nerves from the brain and the subesophageal ganglion. As far as these features are concerned, the observations here presented for *Gelastocoris* are in general agreement with those of other workers, and no unusual conditions have been noted. The appearance and function of the thoracic nerves, on the other hand, has been generally neglected in previous studies, the most detailed account to date being that of Johansson (1957). Since the thoracic nerves were treated in some detail in the present work, a few general remarks may be made concerning them.

The thoracic nerves exhibit, in *Gelastocoris*, a high degree of serial homology. Each of the six nerves innervates comparable structures in each of the three thoracic segments. Some minor differences may be observed between the prothorax and the pterothorax, the nerves of the latter supplying structures associated with flight, which are absent in the prothorax. The chief function of the first thoracic nerve appears to be the innervation of the dorsal and ventral longitudinal muscles. This is observed in the prothorax and the mesothorax; in the former the dorsal longitudinal muscles move the head and prothorax, while in the latter they are indirect flight muscles. Dorsal and ventral longitudinal muscles are absent in the metathorax, and in that segment the first nerve does not innervate any muscles. In the two pterothoracic segments the first nerve also supplies the membrane of the wing and innervates the scolopophorous sense organ.

The second thoracic nerve in all three segments innervates the muscles which move the leg forward. In the prothorax it also supplies two small muscles, *Mm. procpisterno-postoccipitales primus et secundus* (*10A*, *10B*) which move the head. In the mesothorax the second nerve innervates the dorsoventral indirect flight muscle, *M. dorsoventralis primus* (*34*); the corresponding dorsoventral muscle of the metathorax, *M. dorsoventralis* (*60*), is, however, supplied by the first abdominal nerve. The third thoracic nerve of all three segments runs into the coxa, goes to the intrinsic levator muscle of the trochanter, and sends a branch to the sixth thoracic nerve. The extrinsic depressor muscles of the trochanter are innervated, in all three segments, by the fourth thoracic nerve.

The muscles which move the leg backwards are associated with the fifth thoracic nerve; in the two pterothoracic segments this nerve also supplies the direct flight muscles. Finally, in all three segments the sixth nerve is the main nerve of the leg, and is the largest in size.

Although Johansson (1957) described the thoracic nerves of *Oncopeltus* only briefly, his illustrations make possible a comparison with *Gelastocoris.* He distinguished three main nerves in each segment, the anteriormost corresponding to the first nerve of the present study. Among the two more posterior nerves of *Oncopeltus* five branches can be recognized which correspond to the last five thoracic nerves of *Gelastocoris.* The paths of these branches and the structures which they innervate appear to be nearly the same as those of *Gelastocoris,* and a similar plan of serial homology is evident.

A few minor differences between *Gelastocoris* and *Oncopeltus* may be noted. In the latter, Johansson observed a pair of small ''sternal nerves'' coming from the ventral parts of the prothoracic and mesothoracic ganglia. These were not seen in *Gelastocoris.* Dorsal and ventral longitudinal muscles are present in the metathorax of *Oncopeltus* but absent in that of *Gelastocoris.* In *Oncopeltus,* the dorsal muscles are innervated by a branch of the first metathoracic nerve, whose general appearance resembles the branch of *nervus metathoracicus primus* going to the metanotum of *Gelastocoris.* A third difference is the fusion, in *Oncopeltus,* of all but the anteriormost metathoracic nerve into a common trunk representing the second through sixth nerves of the present study. In the metathorax of *Gelastocoris,* as in the prothorax and the mesothorax, these five nerves come off in two distinct groups.

A few features of the gelastocorid nervous system may help to shed some light upon the phylogenetic position of this group. Most authorities on heteropteran phylogeny agree that the Gelastocoridae, along with two other littoral families, the Ochteridae and Saldidae, represent a stage in the evolution of the totally aquatic and semi-aquatic bugs from the terrestrial Heteroptera. Whether the Gelastocoridae are more closely related to the totally aquatic bugs or to the semi-aquatic forms is not, however, generally agreed upon.

According to the system of classification which groups the semi-aquatic and terrestrial bugs into the Gymnocerata (Heteroptera with long, free antennae) and the totally aquatic families into the Cryptocerata (Heteroptera with reduced, concealed antennae), the Gelastocoridae, whose antennae are small and hidden, should be included in the latter group. China (1955) considered them to be offshoots from the primitive ancestor of the totally aquatic bugs, having arisen before the ancestral form became aquatic. Spooner (1938), however, who used Dufour's (1833) terminology of Hydrocorisae (totally aquatic bugs), Geocorisae (terrestrial bugs), and Amphibicorisae (semi-aquatic bugs), believed the gelastocorids to be most closely related to the last group. For a more detailed discussion of this problem and for a brief review of the theories of other authors, the reader is referred to my earlier paper (Parsons, 1959).

The nervous system of *Gelastocoris* shows some features of both the Hydrocorisae and the Amphibicorisae. Perhaps the most obvious similarity to the totally aquatic bugs is seen in the pattern of fusion of the ganglia of the central nervous system. Both Brandt (1878) and Pflugfelder (1936-37) have studied the various types of fusion of these ganglia in representatives of several heteropteran families. In the Amphibicorisae, all the ganglia posterior to the brain are merged into a more or less single mass ("*Hydrometra*"=*Gerris*, Brandt, 1878; *Gerris, Velia, Hydrometra,* Pflugfelder, 1936-37; *Hydrometra,* Sprague, 1956). In most Geocorisae there is less fusion, the subesophageal ganglion, and usually the prothoracic ganglion as well, being independent from the rest of the ganglia; this was observed in several Geocorisae by Brandt (1878) and Pflugfelder (1936-37), in *Leptocorisa* by Akbar (1958),and in *Rhodnius* by Wigglesworth (1959). The Hydrocorisae, however, are characterized by the fusion of the subesophageal ganglion with the prothoracic ganglion. This has been observed in the Nepidae (Brandt, 1878; Pflugfelder, 1936-37; Hamilton, 1931; Graichen, 1936), the Naucoridae (Pflugfelder, 1936-37; Rawat, 1939), the Notonectidae (Brandt, 1878; Pflugfelder, 1936-37), the Belostomatidae (Pflugfelder, 1936-37), and the Corixidae (Pflugfelder, 1936-37).

In *Gelastocoris* the subesophageal and prothoracic ganglia are fused into one mass which is separated from the more posterior ganglia. In this respect it resembles the Hydrocorisae rather than the Amphibicorisae. These distinctions between the three heteropteran groups are not clear-cut, however, since there are some exceptions; the terrestrial bugs *Cimex* (Pflugfelder, 1936-37; "*Acanthia*" of Brandt, 1878), *Calocoris* (Pflugfelder, 1936-37), and *Capsus* (Pflugfelder, 1936-37) show the same pattern of fusion as the Hydrocorisae. In *Nezara* the longitudinal connectives between the subesophageal and prothoracic ganglia and between the prothoracic and posterior ganglia appear to be fused medially (Malouf, 1933). The central nervous system of this terrestrial insect approaches the form seen in the Amphibicorisae, but the boundaries between the ganglia are much more evident externally in *Nezara* than in the semi-aquatic bugs.

The histology of the brain reveals a few other similarities between *Gelastocoris* and the Hydrocorisae. The two-layered condition of the *lamina ganglionaris* and the probable presence of four strata in the *medulla externa* is characteristic of the Hydrocorisae but not of the Amphibicorisae or Geocorisae, according to Pflugfelder (1936-37). That author also stated that the *tractus olfactorius* is more weakly developed in the Hydrocorisae than in the Geocorisae. (He included the Amphibicorisae, which he termed collectively the "Hydrometridae", in the latter group.) This tract appeared to be considerably more weakly developed in *Gelastocoris* than in the Geocorisae illustrated by Pflugfelder (1936-37). The absence of a ventral glomerulus in the corpus pedunculatum of *Gelastocoris* appears, however, to link it with the Amphibicorisae; Pflugfelder was unable to find this glomerulus in any of his "Hydrometridae." Unfortunately, he did not mention whether or not it is present in the Hydrocorisae. The deutocerebrum of *Gelastocoris* shows similarities to both the Hydrocorisae and the Amphibicorisae. It is generally weakly developed, and its sensory portion shows no distinct central fibrous mass; both these features are characteristic of the totally aquatic and semi-aquatic bugs, as distinct from the terrestrial Heteroptera, according to Pflugfelder.

A few features of the endocrine glands of *Gelastocoris* may be of phylogenetic significance. In general, the corpus allatum resembles that of the Amphibicorisae and Geocorisae, while the corpora cardiaca are more like those of the Hydrocorisae. The single, median corpus allatum links the gelastocorids with the former two groups. The general appearance of the corpora cardiaca, however, is more like that of the Cryptocerata than that of the Gymnocerata as figured by Cazal (1948). Three other features which Cazal claimed to be characteristic of the endocrines of the Cryptocerata are seen in *Gelastocoris*: the two-part histological division of the corpus cardiacum, the position of this gland relative to the aorta and the dorsal pharyngeal dilator muscles, and the nature and distribution of the fibro-glial tissue.

It appears, therefore, that although the nervous system of *Gelastocoris* bears some resemblances to that of both the Amphibicorisae and the Hydrocorisae it has more features in common with the latter group than with the former. The deutocerebrum and the endocrine glands show characteristics of both groups; the histology of the protocerebrum and the general form of the central nervous system, however, are more similar to the Hydrocorisae. This is in agreement with the conclusion reached in the previous studies of the head (Parsons, 1959) and the thorax (Parsons, 1960), that the closest living relatives of the Gelastocoridae are to be found among the totally aquatic Heteroptera.

EXPLANATION OF FIGURES

In most of the drawings of dissections, the diameters of the nerves have been somewhat exaggerated in order to make them stand out. The cephalic and thoracic muscles are indicated by the numbers listed below; the numbers of the cephalic muscles are preceded by an "H."

The abbreviations used in the figures are as follows:

A — first branch of *nervus prothoracicus tertius*
AII-VII — second-seventh abdominal segments
AL — accessory lobe of protocerebrum
AO — aorta
AS — antennal socket
AXII, III — third axillary sclerite; mesothorax, metathorax
B — second branch of *nervus prothoracicus tertius*
BR — brain
C —circumesophageal connective
CA— corpus allatum
CAD — dorsal commissure of accessory protocerebral lobes
CAV — ventral commissure of accessory protocerebral lobes
CB — central body
CBD — dorsal body of central body
CBT — tubercle of central body
CBV — ventral body of central body
CC — corpus cardiacum
CCA — anterior part of corpus cardiacum

CCP — posterior part of corpus cardiacum
CD —deutocerebral commissure
CE — *chiasma externum*
CI — *chiasma internum*
CR — commissure of roots of corpora pedunculata
CT — tritocerebral commissure
CTB — commissure of *tubercula optica*
CX— coxa
D — deutocerebrum
EII, III — epimeron; mesothorax, metathorax
EP — epipharyngeal plate
FI, II, III — furca; prothorax, mesothorax, metathorax
FC — frontal commissure
FP — food pump
FT — fibro-glial tissue
G — gut
GA — fused abdominal ganglia
GB — globuli cells of corpora pedunculata
GF — frontal ganglion
GH — hypocerebral ganglion
GMS — mesothoracic ganglion
GMT — metathoracic ganglion
GP — posterior ganglion
GPR — prothoracic ganglion
GS — subesophageal ganglion
H — head (number following indicates a cephalic muscle, as listed below)
HW — hypopharyngeal wing
L — lateral body (?)
LC — longitudinal connective
LG — *lamina ganglionaris*
LV — mandibular lever
M — pericoxal membrane
MD — motor part of deutocerebrum
M.DV — dorsoventral abdominal muscle
ME — medulla externa
M.GT — *M. glandulae thoracicae*
MI — *medulla interna*
ML — main lobe of protocerebrum
MS — mandibular stylet
M.VL — ventral longitudinal abdominal muscle
N — nerve (see list below)
NTII, III — notum; mesothorax, metathorax

OL — optic lobe
P — protocerebrum
PAI, II — pleural apophysis; prothorax, mesothorax
PB — protocerebral bridge
PHII, III — phragma; mesothorax, metathorax
PI — pars intercerebralis
R — roots of corpora pedunculata
RP — *ramus posterior*
RS — *ramus superior*
S — afferent salivary duct
SD — sensory part of deutocerebrum
SK — stalk of corpus pedunculatum
SP — salivary pump
ST — sternum of prothorax
T — tendon (number following indicates muscle, as listed below, inserting on tendon)
TB — *tuberculum opticum*
TC — *tractus chiasmaticus*
TL — tracheole
TN — trochanter
TO — *tractus olfactorius*
TOA — *tractus opticus anterior*
TOM — *tractus opticus medialis*
TOP — *tractus opticus posterior*
TR — tritocerebrum
VP — ventral process of mesothoracic phragma

Muscles

H8 — *M. protractor setae mandibularis primus*
H9 — *M. protractor setae mandibularis secundus*
H10 — *M. retractor setae mandibularis primus*
H11 — *M. retractor setae mandibularis secundus*
H12 — *M. protractor setae maxillaris*
H13 — *M. retractor setae maxillaris*
H14 — *M. dilator cibarii primus*
H15 — *M. dilator cibarii secundus*
H16 — *M. dilator cibarii tertius*
H17 — *M. dilator cibarii quartus*
H17A — *M. dilator praepharyngis*
H18 — *M. dilator postpharyngis ventralis*
H19 — *M. dilator postpharyngis dorsalis*
H20 — *M. levator scapi*

H21 — *M. depressor scapi*
H24 — *M. dilator oris glandulae capitis*
H25 — *M. retractor pistilli*
M.DV — dorsoventral abdominal muscle
M.GT — *M. glandulae thoracicae*
M.VL — ventral longitudinal abdominal muscle
1 — *M. pronoti primus*
2 — *M. pronoti secundus*
3 — *M. pronoti tertius*
4 — *M. pronoti quartus*
5 — *M. pronoti quintus*
6 — *M. prosterni primus*
7 — *M. prosterni secundus*
9 — *M. dorsoventralis*
10A — *M. proepisterno-postoccipitalis primus*
10B — *M. proepisterno-postoccipitalis secundus*
13 — *M. noto-trochantinalis*
14 —*M. noto-coxalis primus*
15 — *M. noto-coxalis secundus*
16 — *M. noto-coxalis tertius*
17— *M. pleura-coxalis*
20A — *M. noto-trochanteralis primus*
20B — *M. noto-trochanteralis secundus*
21 — *M. pleura-trochanteralis*
24(A), (L), (P) — *M. coxa-trochanteralis lateralis;* anterior, lateral, posterior bundles
30 — *M. mesonoti primus*
31— *M. mesonoti secundus*
32 — *M. mesosterni primus*
34 — *M. dorsoventralis primus*
35 — *M. dorsoventralis secundus*
38 — *M. episterno-alaris*
40 — *M. noto-trochantinalis*
41 — *M. noto-coxalis*
42 — *M. episterno-coxalis*
46 — *M. noto-trochanteralis*
47A — *M. pleura-trochanteralis primus*
47B — *M. pleura-trochanteralis secundus*
48 — *M. furca-trochanteralis*
60 — *M. dorsoventralis*
61 — *M. episterno-alaris*
63— *M. noto-trochantinalis*
64 — *M. noto-coxalis*

65 — M. furca-trochantinalis
66 — M. episterno-coxalis
67 — M. coxa-subalaris
70 — M. noto-trochanteralis
71 — M. pleura-trochanteralis
72 — M. furca-trochanteralis
80 — M. ventralis abdominalis

Nerves

N.A — nervus antennalis
N.ABI-V — nervi abdominales; primus-quintus
N. AM — nervus antennalis, motor branch
N.CA — nervus corporis allati
N.CCI,II — nervus corporis cardiaci; primus, secundus
N.CM — nervus capitis-mesothoracicus
N.CP — nervus capitis-prothoracicus
N.F — nervus frontalis
N.FL — nervus frontolabralis
N.L — nervus labralis
N.LA — nervus labialis
N.LT — nervus lateralis
N.MI-VI — nervi mesothoracici; primus-sextus
N.MDI,II — nervi mandibulares; primus, secundus
N.MTI-VI — nervi metathoracici; primus-sextus
N.MXI-III — nervi maxillares; primus-tertius
N.O — nervus ocellus
N.OP — nervus opticus
N.PI-VI — nervi prothoracici; primus-sextus
N.PM — nervus protractoris mandibularis
N.PR — nervus procurrens
N.R — nervus recurrens
N.TI, II — nervi tegumentarii; primus, secundus
N.TR — nervus tritocerebralis

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ON BURMESE EARTHWORMS OF THE FAMILY MEGASCOLECIDAE

By G. E. Gates
University of Maine, Orono

CAMBRIDGE, MASS., U.S.A.
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No. 6 — *On Burmese earthworms of the family Megascolecidae*[1]

By G. E. Gates

University of Maine, Orono

CONTENTS

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[1] From a manuscript written during tenure of a John Simon Guggenheim fellowship.

INTRODUCTION

This contribution completes publication of results of the author's study of megascolecid earthworms collected in Burma during 1923-1941. Determination of relationships has been seriously handicapped by loss of much unpublished information (as well as of most Burmese collections) during World War II. Since then only a few Burmese specimens have been available and they were considered elsewhere. Collections from several places in India and from other regions have provided some of the desired data. Information now recorded does, however, provide further confirmation for previously published conclusions (cf. Discussion) as to inadequacies of the classical system of the Oligochaeta and as to the great importance, both for taxonomy and phylogeny, of formerly neglected portions of the somatic systems.

SYSTEMATICS

Family MEGASCOLECIDAE

Redefinition of this family (Gates, 1959) excluded several genera. With those exceptions, the family is equivalent to the Megascolecidae of Michaelsen's classification (1921). Excluded genera, all with tubular prostates of ectodermal origin, were transferred to the Acanthodrilidae or Octochaetidae, according to holonephry or meronephry, respectively, of the excretory systems. *Plutellus,* formerly in the Megascolecidae of Michaelsen or the Megascolecinae of Stephenson (1930), is now in the Acanthodrilidae and will have to be considered in another article.

Genus PERIONYX Perrier, 1872

This classical genus comprises, in addition to peregrine forms that have been carried from the Orient all around the world by man, species endemic in Ceylon, India, Burma, Australia and New Zealand. The gap in the distribution, though not as great as in the case of *Notoscolex* and *Megascolex* (long notorious for morphological heterogeneity and polyphyly), is large enough to invite reconsideration of the status of the genus. Random sampling of a few species descriptions, each much too perfunctory for present needs, shows that somatic structure of the genus would have to be characterized somewhat as follows: Setae, lumbricin anteriorly or perichaetin throughout. Digestive system, with one or two gizzards or none — with calciferous glands of varied or unknown structure in various segments of the region from vii to xiv or without calciferous glands. Vascular system, with paired or unpaired dorsal trunk, with esophageal or latero-esophageal or lateral hearts in region of x-xiii. Excretory system, holomegaphridial or meromeganephridial, or with micronephridia alongside meganephridia posteriorly. Characterization of genital structure might require addition of the following: Prostates racemose and of mesoblastic origin, or tubular and of ectodermal origin. Whether defined as by Stephenson or as by Michaelsen on any one of several occasions, *Perionyx* obviously is a congeries lacking the over-all similarity of anatomical structure that should be expected in species so closely related as to belong together in a monophyletic genus.

Descriptive matter provides a major portion of the generic definition in its terminal classical form: Setae in rings often almost closed. Male pores often approximated in greater or less degrees, and may be very close to the middle line. Spermathecal pores like the male pores often very near the middle line, the last pair in 7/8 or 8/9. Gizzard frequently more or less vestigial, in v or vi. Two pairs of testes and funnels. Such statements, even when incomplete or not misleading, are not definitive. The meroandric *P. rufulus* Gates, 1945, for instance, provides one more example of the folly of defining genera by genital characters liable to rapid evolutionary modification, except in strict accordance with over-all somatic similarity.

The type species, *excavatus,* is of Indian origin. Accordingly, search for over-all similarity by which the genus must be defined can be restricted, initially at least, to southeast Asian species that are likely to be congeneric with *excavatus.* Unfortunately, most oriental species have been known hitherto only from descriptions of a holotype or of a short series secured at a single site. Some of the types were known to be abnormal and others assumed to be normal are now under suspicion. Some certainly are immature; at least one is much too juvenile to permit recognition of genital characters by which species must be mainly defined and distinguished from each other. Although an occasional type was old enough to have matured sperm, few if any seem to have had the clitellar tumescence that indicates attainment of the breeding stage.

Location of the gizzard is mentioned in previous species descriptions, usually with some additional characterization such as: recognizable only in sections, vestigial, rudimentary, very small, small, moderately large or large but soft. Although presence of a gizzard with some special muscularity and in v or in vi would seem to be required by the generic definition, at least four species lack any vestiges and another is supposed to have one in vii. Some intraspecific variation also is indicated by the literature, both as to presence or absence and as to location in v or vi. The organ probably was often characterized, because of reluctance to damage a type, from its external appearance in a dissection. However, free-hand sections, with scissors or other instruments, sometimes show that external appearances are quite misleading. Such sections of an anterior portion of the esophagus in field-preserved material of *excavatus* provided so much divergence in laboratory records, both as to presence or absence and location that any mention of a gizzard is omitted from the description below. Regardless of how much use the gizzard may prove to have in defining species, the organ obviously cannot provide any such generic characterization as in *Pheretima* and *Eutyphoeus.* Over-all similarity, insofar then as digestive organs are concerned, must be sought in the remaining portion of the system.

Calciferous glands definitely are lacking in many species, according to previous descriptions. Omission of any mention of the glands usually is attributable to lack of interest in recording absence. None have been found in any species examined by the author. Nevertheless, calcium secreting tissues are present and fine granules or larger concretions have been found, not only in all species that have been available alive but also in others examined not too long after preservation. Calciferous tissues apparently are located, in low irregular ridges or higher folds that may be more or less lamelliform, within a portion of the esophagus centering at xiii. Some interspecific variation in segmental location is indicated in the literature but field-preserved material is unlikely to provide, even from microtome sections, data needed for species characterization. Only a negative character, absence of discrete glands, is available for generic definition. The segment in which the intestine begins was mentioned in many of the earlier descriptions but none of the authors display knowledge of the difficulties attendant on the determination. Considerable variation is obvious and generic characterization, such as for *Eutyphoeus*, certainly is impossible. Much of the intraspecific variation that has been found (cf. *bainii* and *excavatus*) is attributable to a process (considered below) some knowledge of which is needed by biologists who may have occasion to study any perionyx. Evidence for existence of intestinal caeca and typhlosoles or supra-intestinal glands is lacking in the literature and none of those organs were found in the many specimens that have been examined by the author during the last thirty years. Over-all similarity, insofar as the digestive system is concerned, seems to be limited to negative characters.

The circulatory system was considered of no evolutionary importance for the phylogenies on which the classical system came to be based. Hence, older systematic contributions often provide no information about it. Nothing at all is known about the system in three species of *Perionyx*, and for others all that is recorded is position of the last pair of hearts. They are, so far as is known, either in xii or xiii, possibly with very little normal intraspecific variation. The vascular system, except as just indicated, has been found to be macroscopically identical in all species the author has studied. Such invariability, in the circumstances prevailing, invites an assumption of similar uniformity in other species of the genus. However, just as in case of the hearts, normal must be understood.

The emphasis on normality is required because of a regenerative capacity unequalled in earthworms except in the European *Criodrilus lacuum*. Proof that such capacity often is invoked was secured in India. Collections obtained there during a period of three years contained 150 specimens of *millardi* Stephenson, 1915, with head and 175 with tail regenerates, 499 of *sansibaricus* Michaelsen, 1891, with head and 1200+ with tail regenerates. Each head regenerate still was externally distinguishable from its substrate by differences in pigmentation and segment size. These external stigmata of regeneration were found, in laboratory experiments, to disappear shortly in case of heads but not tails where obvious differences in pigmentation still remain after a period long enough to permit terminal regeneration a second or even a third time. Older cephalic regenerates (according to data obtained from operations in the laboratory, at known levels and under controlled conditions, if substrates were sufficiently mature or later became mature) are externally identifiable by homoeosis of the clitellum and reproductive apertures. After exclusion of all specimens with recent cephalic regenerates (indicated by pigmentation and segment-size differences) from 8 series comprising 117-1235 specimens of *P. sansibaricus* (total. 3252), incidence of homoeotic individuals was found to vary from 6.1 percent to 14.4 percent. Comparison of the anatomy of natural cephalic regenerates (including homoeotics) with that of several thousand experimentally obtained regenerates provided a number of generalizations, some of which are of special importance in the taxonomy of *Perionyx*. Homoeosis, in interest of simplicity and brevity, is indicated by reference to but one of the three species that were studied experimentally, *P. sansibaricus*. This is characterized as follows: spermathecal pores, 3 pairs, anteriorly in vii-ix; clitellum, on xiii-xvii; female pore, median, in xiv; clitellum, on xiii-xvii; male pores, each in a special area or tumescence within a single field, in xviii; gizzard, in v; calciferous widening of esophagus, in xiii; intestinal origin, in xvi; latero-esophageal hearts in x-xii; testes, in x-xi; ovaries, in xiii; spermathecae, with a single stalked diverticulum.

Rapid formation of a new head is possible by any substrate comprising more than the last fifty segments of the original soma. Shorter substrates, in favorable conditions, may also produce a new head.

All organs of a pre-intestinal region of the body may be developed in epimorphic regeneration. Male terminalia always, other genital organs occasionally, are formed during morphallactic reorganization in a proximal portion of the substrate.

Spermathecal pores may be lacking, or unpaired and then in normal location, or at mV, or (only in morphallaxis) in other unusual position, or paired and then in 1-7 segments (nearly always consecutive) of iii-xii. Spermathecae may be more or less completely bifid when median, normal, adiverticulate or with two or more diverticula. A mature spermatheca with spermatophore projecting to the exterior from the pore may be moved forward unchanged into an apparently epimorphic regenerate. Spermathecae without spermatophores were more or less completely histolyzed during migration. A battery of six spermathecae in normal segmental locations was present only in 3 of 52 thecal regenerates at levels 11/12-17/18.

Female pores may be pre- or intra-clitellar, median and unpaired, paired or lacking even though female gonoducts are well developed, in 1-4 segments (usually consecutive) of vi-xviii. Ovaries may be present in 1-4 segments of v-xvii.

The clitellum may comprise 2-15 of the segments from v to xxvi. It is always annular.

Male fields may be lacking, asymmetrical or symmetrical, in 1-12 of segments ix-xxvi; when more than one is present they are usually in consecutive segments. Male terminalia may be lacking even if one or more male fields are present; when formed they usually are in but one of the segments with a male field.

A gizzard may be lacking (often), of subnormal muscularity, in any of segments iii-vii. A calciferous widening of the esophagus may be lacking (often), longer than usual, in any of segments ix-xvii. Intestinal origin may appear to be in any of segments ix-xxvi. A portion of the intestine in the proximal part of the substrate often loses the characteristic brown coloration and becomes much narrower, often valvular in appearance. Similar narrowing of an anterior portion of the intestine may take place in fasted animals that are not regenerating, or at height of sexual functioning, seemingly because of compression by prostates.

Latero-esophageal hearts may be present in 1-7 of segments vi-xvi, usually in uninterrupted series, usually paired, one of the last pair occasionally lacking. The six major blood vessels (dorsal, ventral, supra-esophageal, extra-esophageal [2] and subneural trunks) are present, and the last-named extends nearly to the anterior end of the regenerate. Rarely, the dorsal trunk is doubled in a short stretch or resolved into a plexus. Smaller vessels and vascular networks usually show differences from species norm. Divergence from that norm is lacking in the excretory system. The nervous system appears to be normal macroscopically, except in monstrosities. The brain of short heads regenerated at really posterior levels may be in ii or i.

Testes may be 1-5 pairs in segments iv-xv. The gonad series usually is uninterrupted in longer regenerates. Testis:ovary ratios usually are divergent from species norm (4:2), for instance, 2:2 in shorter regenerates, 2:6, 6:6, 8:8, 10:2, 10:6, etc., in longer regenerates. Gonads in a middle portion of the series may be hermaphroditic. Sperm and mature ova have been found in the same segment. Female gonoducts may unite in the parietes to open by a single median pore or may acquire individual apertures. Female gonoducts that do not acquire external openings in the segment behind the septum bearing the funnels may turn laterally and join the male gonoducts. Ducts from male funnels may unite in the parietes and open to the exterior through a median aperture indistinguishable from the female pore. (Number and location of ovaries accordingly cannot be determined from position of female pores as sometimes has been assumed.) Some homoeotic individuals not only had matured sperm profusely but in spite of markedly aberrant anatomy had copulated successfully as was proved by presence of sperm in the spermathecae. Aclitellate homoeotics, mature enough to have sperm on their male funnels, also had copulated. Ovaries with apparently mature ova occasionally were found in homoeotics in which no slightest race of clitellar development was recognizable.

Regeneration, in either direction, is possible from the day the young worm emerges from the cocoon. Homoeosis of male field rudiments in juveniles too young for other genital structures to be recognizable may have resulted from regeneration at an earlier stage.

Permutations and combinations of structure, as indicated above, are so numerous as to indicate, especially when finer structure is taken into consideration, that few head regenerates will be identical. Certainly little uniformity was found in regenerates formed at the same level in the laboratory by worms of as near the same age and condition as could be determined by external inspection under anesthesia.

The somatic anatomy that now appears, from normal worms, to be uniform throughout the genus also characterizes regenerates whether cephalic or caudal. Divergence from species norms in the regenerates is very largely restricted to structure by which species must be identified, defined and distinguished from each other.

In concluding this brief statement of regenerative capacity one of the records illustrative of the remarkable viability of a perionyx is cited. A worm that escaped from its container sometime after the laboratory had been closed for the night was coiled up, the next morning, in full glare from an unclouded hot-season tropical sky. The body was stiff but not brittle enough to break on slight bending. After a few moments in water the anterior half began to jerk back and forth convulsively. Movements shortly ceased and the worm was then placed on a saturated towel in a tightly closed container. The next day, anterior and posterior portions (no indication of autotomy anywhere) were flattened, almost liquefied, giving off an odor that testified to certainty of advanced decay. A middle portion had not yet collapsed and appeared to be normally turgid though unresponsive to slight stimuli. Dead portions were excised so as to leave a fragment (of 22 segments) which in three weeks produced a head regenerate of thirteen segments, anteriorly, and a tail regenerate, posteriorly.

Excretory organs, not even mentioned in descriptions of several species, usually were said to be meganephridial, sometimes with an additional notation such as, "nephridia end in the same line." *Perionyx* has been defined, in effect at least, for 65 years as meganephridial. Hence, mention of a generic character in a species description presumably was not always thought to be necessary. Presence of micronephridia in addition to large nephridia usually has been mentioned in other genera. The only instance in *Perionyx* (cf. *annulatus* below) needs no further consideration here. The excretory system in *Perionyx* now appears to vary interspecifically only with reference to location of nephropores and shape of the vesicles when they are present. The only exception, as to number per segment, is provided by Himalayan giant forms (cf. *annandalei* below).

"Meganephridial" originally meant presence per segment of two nephridia each with a preseptal funnel and a postseptal looped tubule opening in its own metamere to the exterior through an epidermal aperture. An excretory system composed of such units, in modern terminology, is holonephric. The Himalayan giants have several nephridia per segment. These, however, are not micronephridia but are of the same kind as the paired nephridia of other species. The two kinds, in modern terms, are distinguished from each other as meromeganephridia and holomeganephridia. Difference in number does not appear at present to warrant even subgeneric separation in view of the over-all similarity of somatic anatomy.

Large enteronephric meronephridia — especially when paired as in *Lampito*, and the larger median member of a transverse row of nephridia — as in the post-typhlosolar segments of *Eutyphoeus*, often have been called meganephridia. That term, in the definition below (p. 216), is replaced by a more precise characterization in the hope of avoiding some of the confusion that has prevailed in the past.

The meronephry of the Himalayan giants is assumed to have arisen by longitudinal splitting of each of the two embryonic anlagen per segment. Such splitting, when restricted to preseptal portion of the anlage, presumably has been responsible for the multiple funnels that are recorded from various genera. True integumentary micronephridia arise in another way, by transverse fragmentation of the postseptal portion of the embryonic tubule, and hence are astomate. Such micromeronephridia are so different from meromeganephridia in morphology, ontogeny and phylogeny as to indicate relationships to other genera than *Perionyx*.

Passage of nephridial ducts into the parietes, on each side of the body, in a single more or less regular line may not be proof that external apertures are in a single rank. In certain lumbricids, for instance, some of the ducts open well lateral to the level at which they enter the musculature. Information is needed for species characterization not only as to real locations of the nephropores but also as to presence of vesicles and their shape — in one species the shape appears to vary according to the level at which the pore is located.

Generic uniformity in reproductive systems is restricted to the racemose prostates characteristic of the family and, possibly, median union of oviducts. The classical definition says, "Female pore unpaired (? always)." The parenthetical question presumably refers to *P. foveatus* Stephenson, 1914, in which pairing was suspected though actual pores were not seen. Oviducts in regenerates occasionally do not unite. Coelomic cavities of testis segments in *Perionyx* are filled, at maturity, with a very sticky material that hardens into a firmly coherent mass on preservation. Masses of such coagulum, even in microtome sections and in various species of several genera, have been mistaken for seminal vesicles. A horseshoe-shaped mass of coagulum adherent to the anterior face of 10/11 in *koboensis* Stephenson, 1912, may have been mistaken for a pair of dorsally united seminal vesicles. Loosened peritoneum adherent to the coagulum conceivably could have appeared to be the wall of a testis sac in several species. Male genital apertures rarely have been seen, and are not even in clefts or grooves that were thought to be the male pores. The real situation in *excavatus* was found only when tension on adjacent epidermis separated tightly apposed lips.

Pigment in all species that have been seen alive is red, though the dorsum sometimes appears to be dark blue or even almost black. A green color that may be characteristic of two species is not localized (as also in several species of *Pheretima*, *Eutyphoeus* and *Allolobophora*) in visible granules. The green color shortly disappears in alcohol and in formalin.

Characters that have been found, regardless of species, to be uniform in regeneration homoeotics as well as in normal individuals are assumed to be generically definitive. Lack of information for species that have been unavailable requires the revised definition below to be labelled tentative for the present.

A hypothetical ancestral protoperionyx from which extant species might have evolved is characterized as follows: Prostatic, female and spermathecal pores minute and superficial. Dorsal pores present from 1/2. Digestive system with a gizzard in v and intestinal origin in xii. Excretory system holonephric, without cephalization. Holandric. Seminal vesicles in ix-xii. Spermathecae, without seminal chambers or diverticula, two pairs, opening at 7/8-8/9. Other characters as in definition below.

Absence of calciferous glands, intestinal typhlosole, caeca and other glands presumably is primitive, and most of the gut has remained in that condition throughout the genus. Absence of a gizzard, in some species, may be an illustration of secondary simplification, as classical authorities seem to have agreed that presence of the organ is "a primitive feature in all families of the Megadrili." Retention, without modification, of typical holonephridia in ii and the next few segments also appears to be primitive, at least in comparison with many of the genera now or formerly included in the Megascolecidae. If a complete series of dorsal pores is primitive, there has been very little cephalization of that system in *Perionyx*. Major blood vessels are the same as in *Pheretima* but so little is known about the comparative anatomy of the vascular system in earthworms that only presence of uninterrupted dorsal and ventral trunks can be called primitive. Absence of spermathecal diverticula appears to be primitive, as also in the Moniligastridae and the Ocnerodrilidae. The only specialized characters imputed to the protoperionyx are the perichaetin setae (shared with an ancestral pheretima) and the peripheral union of female gonoducts (probably not shared).

Intrageneric evolutionary developments can be summarized as follows: Transfer of gizzard into vi (common), possibly later on into vii (once?); weakening of the muscles (even when the layer is thick) if the primitive organ really was strong; decrease in thickness of the circular muscle layer (very common) ending eventually (several times) in disappearance of the gizzard. Elongation of the esophagus (common), perhaps in association with posterior extension of calciferous tissues. Addition of a pair of hearts in xiii (independently in Burma, the Deccan, and in the Himalayas). Separation of each nephropore rank into a dorsal and a ventral rank (four times in peninsular India, once in the Himalayas). Increasing irregularity in the single rank may indicate an early trend in direction of the two-rank condition. Enlargement of an ectal portion of the nephridial duct into a vesicle (in three of the peninsular species with nephropores alternating irregularly between two ranks, once in a Himalayan species without alternating pores). Increase in number of nephridia (once, in the Himalayas).

Testes and male funnels of x have been eliminated (once, Assam). Seminal vesicles of ix have been eliminated in all species except *minimus* Stephenson, 1920, those of x in all except *koboensis*, those of xi in *rufulus*. Small chambers have appeared in an ental portion of the spermathecal duct of various species (and perhaps more commonly than has been recognized). They are single and of no fixed position, few and scattered, or in rosettes, bands and rings. One or two stalked diverticula with single seminal chambers have appeared (once each in Burma, the Deccan, South India, possibly in the Malay Peninsula, twice in Ceylon). Better known, of course, because of their use in identification of species, are the changes in number of spermathecae. Addition of a third pair in vii (4 species in the Himalayas, 3 in peninsular India, 1 in Ceylon), elimination of the pair in ix presumably after acquisition of the pair in vii (16 species in the Himalayas, very little known about any of them). Elimination of the pair in ix before a pair had been acquired in vii (2 species, Burma). Acquisition of a pair in vi, presumably after appearance of a third pair in vii (2 species, Burma). One species in Ceylon is supposed to have seven pairs of spermathecae but a hyperplasic battery may have resulted from regeneration. Intermediate stages, of five and six pairs are unknown and the octothecal condition is found only in Burma.

Other changes in the genital system: evolution of intromittent copulatory organs, at least twice (in 3 Himalayan species); evolution of penial setae of a rather generalized type (common); elimination of penial setae (or at least of ventral setae that could have been penial); migration of spermathecal and male pores laterally or mesially; dislocation of spermathecal pores back from the intersegmental furrows (once in the Himalayas, once in the Deccan).

Macroscopically recognizable evolutionary changes, as now known, obviously are much more numerous in the genital than in any other system. Some of the changes may have been made independently in two or more portions of the generic range. Unfortunately, much more information about somatic systems of inadequately characterized species is needed for determination of present and past relationships. Primitive forms certainly live, in the Himalayas, alongside forms that have specialized intromittent organs, an advanced sort of meronephry, modified spermathecal batteries, much larger numbers of setae, and considerably greater soma size. The Himalayas, or more precisely an eastern portion, were thought (Stephenson, 1923, p. 27) to be "the great focus of evolution of species of *Perionyx*." That focus may prove to be part of the area in which the genus originated, for direct derivation from the Australian *Diporochaeta*, as in classical phylogenies, is impossible. Migration, according to available evidence could be only to the west along the Himalayas and to the south through much of Burma and most of India. Absence of endemics in the Gangetic valley suggests passage from Assam-Burma to the Indian peninsula across the "Garo-Rajmahal gap" (where earthworms ought to be collected intensively at the earliest opportunity). However, paucity of colonizations by peregrine forms in the valley may indicate that conditions have become unfavorable to worms with special ecological requirements. Whether Ceylon and the Malay Peninsula were reached without assistance by man remains to be learned.

The single evolutionary trend that has been recognizable throughout the whole genus is derogation of the gizzard. Vestiges may still be identifiable microscopically even in the very few species that were supposed to be gizzard-less. Presumably then, elimination of the gizzard may require much more time than classical authorities believed, for during the period in which thickness of the circular muscle layer was decreasing, more profound changes were made in the genital system such as elimination of a pair of gonads, of a pair of spermathecae or addition of one or more pairs of spermathecae.

Tentative definition of Perionyx. Digestive system, without supra-intestinal and calciferous glands, intestinal caeca and typhlosole, but with calciferous tissues in some portion of the esophagus. Vascular system with complete, unpaired, dorsal. ventral and supra-esophageal trunks, a subneural adherent to the parietes, paired extra-esophageal trunks median to the hearts, latero-esophageal hearts in x-xii. Nephridia with preseptal funnels and postseptal loops that open to exterior in their own segment through epidermal apertures. Setae, numerous, in a circle at equator of each segment from ii posteriorly. Female pore intraclitellar and median. Clitellum, annular, setae retained. Spermathecae pregonadal. Ovaries fan-shaped and with several egg strings. Prostates, racemose, of mesoblastic origin, with ducts joined entally by the vasa deferentia.

Characters that may prove to be uniform throughout the genus: abortion of septa restricted to region in front of v, no septa thickly muscularized; pigment, red; gizzard (when present) in front of 6/7; definite copulatory papillae lacking (genital markings lacking except for modifications of male field and epidermal tumescences in vicinity of spermathecal pores).

Distribution. Burma, Assam, the Himalayas west at least to Simla, peninsular India, possibly also Ceylon and the Malay Peninsula. The original home of *violaceus* Horst, 1893, supposedly in the peninsula, is unknown. The species has been found in the West Indies. (Distribution of three species widely transported by man not included, above.)

PERIONYX ANNANDALEI (Michaelsen, 1907)

Redefinition of *P. m'intoshi* (Gates, 1952, p. 7) left other giant forms in need of a name. The earliest name that may be available is *Perionychella annandalei* Michaelsen, 1907. The nature of the excretory system in the type of that species unfortunately is unknown. The only data that might contra-indicate identification with the Nepalese giants are penetration of prostates into xix, and location of male pores in the setal circle rather than posteriorly. If *annandalei* proves to be specifically distinct, *Lampito dubius* Stephenson, 1916, may be available. The holotype of that species (from Darjiling district) is meronephric and male pores are in a transverse groove behind the setal zone as in the Nepalese worms. The type, only 6 mm. thick (10-15 mm. in sexual giants) and with spermathecae still confined to the parietes, is too juvenile for recognition of important taxonomic characters.

Male terminalia of two Nepal Valley specimens, originally referred to *m'intoshi*, are one segment behind their normal location and are in xix. Other organs may have been in their normal situations. If so, the aberrant condition, it is now clear, could have arisen in several ways. 1) By mutational translocation of developmental potentiality back into somites at the 19th level. 2) By halving of a mesoblastic somite on each side of the body, at any of the 14th to 17th levels. 3) Somite halving on one side and mutational translocation on the other is theoretically possible. 4) As a result of cephalic regeneration (in a variety of ways depending on level of regeneration, age of regenerant and whether or not morphallaxis also is involved). If gonads are hyperplasic, regeneration is very probable and also morphallaxis. The aberrant worms, in less fortunate circumstances, could have become types of a new species defined by location of male terminalia in xix. Indeed, a distantly related Bombay species, *P. pullus* Stephenson, 1920, is known only from the original description of a single individual that does have male terminalia in xix. However, the specimen was believed to be abnormal, but only with respect to location of the terminalia. If regeneration was responsible for the homoeosis, supposedly normal organization could have been divergent from a specific norm in one or more of several ways. A gizzard, for instance, is lacking, but that structure often is not developed in head regenerates of species that have a much greater muscularity of the organ than in most perionyxes. The spermathecal battery could have been defective or even hyperplasic. Although regeneration now seems to be the most probable cause of the *pullus* homoeosis, another possibility must not be overlooked — that location of the male terminalia in xix is a specific character.

Translocation does occur in mutant individuals of another genus, and in the H morph of *Pheretima anomala* male terminalia are in xx.

(PERIONYX?) ANNULATUS Stephenson, 1914

This species is known only from the description of six specimens from two localities. Four were juvenile; one was regenerated posteriorly, one damaged anteriorly (and not described), another much softened, the last homoeotic (male pores in xix). The clitellum of one adult probably is not tumescent though sperm were present on male funnels. The other adult is homoeotic (male pores in xx). The macerated and supposedly normal adult is the one from which the species was defined. *P. annulatus* differs from all oriental perionyxes in the location of the gizzard behind 6/7 (in vii) and in the presence of "a number of minute micronephridia in regular transverse lines, especially ventrally, in the neighbourhood of the meganephridia." Although *Perionyx* was defined as meganephridial, this species was included (without change in generic definition) because "its general habitus is so markedly that of *Perionyx* that it can hardly be doubtful where its relations lie" (Stephenson, 1914). The regenerative capacity (cf. below) that is indicated by the homoeotics also appears to be markedly that of *Perionyx* and hence much greater than in any other oriental genus. Habitus, together with regenerative ability, justify a question as to whether supposed micronephridia really are excretory organs (cf. *excavatus*). Minute, parietal micronephridia in oriental earthworms are astomate, v-shaped and exonephric. If such nephridia are present in *annulatus* the species obviously does not belong in *Perionyx*. If the supposedly normal mature worm had regenerated, as is quite possible though the text provides no evidence for it, gizzard location could be abnormal (as often in cephalic regenerates) and the spermathecal battery could be hyperplasic. If the battery is quadrithecal normally, and especially if the gizzard really belongs in vii, relationships to *m'intoshi* would appear to require consideration.

The abnormalities which include hyperplasic spermathecae and gonads of both sexes, as well as heterogeneous organ homoeosis (e.g., last hearts +2, male terminalia +1, in the juvenile), now are known to arise during cephalic regeneration, which in the present instances may have been at some level behind 13/14 and in part morphallactic. Accordingly, at least fifty per cent of the worms that were available had regenerated. Half of the adults and a third of the series had regenerated anteriorly.

At least two other species are presently known only from original descriptions of short series that contained homoeotic individuals. *P. turaensis* Stephenson, 1923, was erected on five specimens. All organs from spermathecae to male terminalia of one individual are two levels in front of normal location. The homoeosis undoubtedly resulted from hypomeric cephalic regeneration (-2) at some level in front of 10/11. *P. rufulus* was erected on 11 specimens two of which are clitellate. One of them is homoeotic, doubtless as a result of hypomeric regeneration (-1), possibly at 10/11.

PERIONYX BAINII Stephenson, 1915

India

Almora, United Provinces, in wet ground below spring, *ca.* 6000 feet, June, 0-0-15.

Simla, July, ?-2-50. M. Mathur. (100 odd juveniles, quite probably are of the same species.)

External characteristics. Size, 35-55 by 3-4+ mm. Segments (5 specimens), 91-110. Pigmented, dorsum red or apparently dark blue, ventrum in i-iv or v often light red. Prostomium epilobous, tongue open (37 specimens), definitely closed (1), doubtful in others because of presence of slight and possibly adventitious furrows (one such at mD in prostomial tongue may reach to or well towards 1/2 but always is much less marked than in *sansibaricus*). Setae more closely crowded ventrally; viii/11-15, xix/11-13. Nephropores probably in one somewhat irregular rank on each side, at or close to mL. Clitellum, annular, on xii-xviii, much thinner on xvii and xviii, lacking in ventrum of xviii.

Spermathecal pores large, transverse slits, exactly on intersegmental furrows. Female pore presetal at mV. Male pores small, longitudinal slits at segmental equator, just lateral to penial setae, each overhung by a small but definite and rather spheroidal to ellipsoidal tubercle that must be drawn laterally before the pore can be seen. Median to each male pore, tips of 5-9 penial setae are visible, in a circle or in two transverse rows convergent mesially and laterally, sometimes in a shallow, transversely slit-like depression. Male field quite variable in appearance. Four greyish translucent areas usually recognizable median to the male pores, two presetal and two postsetal. The whole field may be depressed and with a tubercle-like tumescence on each lateral wall.

Internal anatomy. Longitudinal muscle band at mD densely pigmented. Pigment, regardless of external appearances, always red. Postclitellar septa without noticeable thickening (22 specimens). Gizzard rudimentary, in v (22). Esophagus much widened and bead-like in xiii, with calciferous ridges on inner wall. Intestinal origin in xv (8), in xvi (14). No typhlosole (22). Circulatory system as usual, the subneural trunk sometimes recognizable as far forwards as iii. Last hearts in xii (22). Nephridia avesiculate, ducts long and slender, passing into parietes in a single rather irregular rank on each side of the body.

Posterior seminal vesicles, not united dorsally, appear to extend into xiii or xiv with ventral margins incised by the septa. Male gonoducts, which pass into ental ends of prostatic ducts, may be along ventral margin of the prostate or imbedded apparently within the gland itself. Penial setae with 9-11 rather irregular and occasionally interrupted circles of elongately triangular spines. The tip appears pointed as the seta rests normally on the slide, often convex on one side and flat or slightly concave on the opposite side. When the shaft is rolled over, the tip appears to be chisel-shaped or truncate, or the terminal margin may be roughened or even slightly indented to a somewhat bifid appearance.

Spermathecae large, reaching into contact with the dorsal blood vessel or even to dorsal parietes. Seminal chambers unrecognizable externally and not seen in free-hand sections of the duct.

Abnormality. Ten of the Almora worms, larger than the others, are athecal. Seminal vesicles are small, vertically placed, on posterior faces of 10/11-11/12. Prostates (9 worms) perhaps slightly smaller than in thecal individuals. Male pores, prostates and their ducts, lacking in the tenth worm in which male deferent ducts had not grown back into xviii. Setae of xviii ventrally are arranged into two discrete groupings just as in normal worms but other portions of a male field are unrecognizable.

Mesoblastic anlage of the prostates may have developed sufficiently to be able to induce rearrangement of follicles that eventually would have become penisetal but only to abort before the male gonoducts in their posterior growth, had reached xviii. Deprived of the attracting stimuli from the prostatic anlage, the gonoducts apparently ceased to grow.

In the current terminology of genital polymorphism, one third of the Almora batch belongs to some sort of H morph, possibly a male sterile one, 60 per cent to an A morph, the remaining specimen to an AR morph. In *Pheretima*, A and AR morphs, so far as is now known, have evolved only after acquisition of ability to reproduce parthenogenetically. Most A and AR morphs are male sterile. Except for the date above, there is no reason for suspecting parthenogenesis in species of *Perionyx.*

Reproduction. Spermatozoal iridescence was lacking on male funnels and in spermathecae of each specimen. Such absence, in clitellate individuals of *Pheretima* would justify an assumption not only of parthenogenesis but also of male sterility. The juvenile condition of the seminal vesicles would provide further support for the assumption. The coagulum usually present in coelomic cavities of x-xi in sexually functioning individuals also was lacking. Neither lot was secured in the season when species with a limited reproductive period (usually toward the end of the monsoon) breed. However, the species that now seems to be most closely related to *bainii* does reproduce throughout the year or at least so much of it as conditions or environment permit.

Regeneration. Anterior amputees and recent anterior regenerates were lacking. Two of the 52 Simla adults (3.8%) were homoeotics, and without the usual external stigmata of epimorphic (these shortly disappear) or morphallactic regeneration. The internal anatomy of the worms and present knowledge of regenerative capacity in other species of *Perionyx* (Gates, 1951, and MSS) permit several interesting deductions, confirmation of which can be expected. 1) Both worms had regenerated anteriorly; one, a head of 9 segments at 7/8; the other, a head of 14 segments at 15/16. 2) Equimeric regeneration is possible at each level back to 14/15. 3) Head regeneration is possible in *bainii* at each level back at least to region of 50/51 and probably much further posteriorly. 4) Reproductive organs, including spermathecae, testes and ovaries, are developed, in appropriate conditions, in head regenerates. 5) A regenerated head, in certain circumstances, will have no spermathecae and/or male terminalia.

6) Vestiges of the male terminalia, similar to those of the abnormal Almora worm characterized above, develop morphallactically during or after regeneration.

Many of the worms, prior to collection, had lost a posterior portion of the body, apparently at an intersegmental level in each case: 25 per cent of the juveniles, 34 per cent of the clitellates, 100 per cent of the aclitellates. Healing of unregenerate worms had been enteroparietal. Numbers of the worms had regenerated posteriorly: 16 per cent of the juveniles, 24 per cent of the clitellates, 50 per cent of the aclitellates. In each case the regenerate was caudal. Level of regeneration ranged from 39/40 to 87/88 in the juveniles, from 32/33 to 93/94 in the adults. Segment number in those regenerates in which rapid growth had come to an end was: 22 at 39/40, 23-35 at 54/55-58/59, 2-16 at 70/71-79/80, 2-13 at 80/81-89/90, 4-11 at 90/91-93/94. Other regenerates still had a large, four-zoned growth region but with terminal anus or had not initiated metameric differentiation.

The data cited above explain, perhaps only in part, why it is so difficult to obtain information as to normal segment number in species of *Perionyx.* Three of the large atheeal Almora worms had tail regenerates, at 32/33, 35/36, and 70/71.

Parasites. A colonial vorticellid-like organism is present on many of the Simla worms. Various sorts of much smaller protozoa, blue-green algae, and other organisms are present on the vorticellids. A similar epicuticular fauna and flora, but much more densely aggregated, was found on many Jubbulpore specimens of *P. millardi.* The epizoa and their associates spread from the substrate onto a regenerate (especially when cephalic) as it develops.

Remarks. The clitellum of two Simla worms probably had regressed after cessation of reproductive activity.

Almora worms were secured at the end of the dry season from a small area that had been kept quite moist by waste water. They were active and presumably had been able to maintain themselves in that state, without diapause, throughout the unfavorable period. Absence of spermatozoal iridescence, at that time of the year, may not be indicative of male sterility in an H morph.

P. bainii has been known hitherto only from the description of two types. Relationships are with *excavatus* rather than with *millardi.*

PERIONYX DITHECA Stephenson, 1931

This species is known only from the original account of four specimens from Thandaung, in the Toungoo Karen Hills. Spermathecal pores are at 7/8 on three of the types, at 6/7-8/9 on the fourth. The specific name suggests that the bithecal battery was regarded as normal for the species. Presence of extra spermatheca (hyperplasia) in species of *Perionyx* usually is associated with other evidence for cephalic regeneration. However, regeneration, in certain circumstances, often does result in a defective spermathecal battery. Relationships of *ditheca,* if one pair of spermathecae is normal, are with the Chin Hills *viridis* Gates, 1933. In spite of the distance between the two areas and the gap between, relationships appear to be close, *ditheca* distinguishable at present only by a slightly greater clitellar extent (through all of xviii instead of ending at 17/18) and absence of penial setae (possibly merely unrecognized?). If *ditheca* really is sexthecal, relationships to be considered are with *variegatus* (Michaelsen, 1907) from Darjiling district and *foveatus* from the Abor country farther to the east in the Himalayas. The Darjiling species is distinguished by a one segment shorter clitellum, wider separation of the spermathecal pores, a more anterior intestinal origin, and perhaps by presence of nephridial vesicles. Large seminal vesicles were said to be present in x but this requires confirmation. The geographically closer *foveatus* is distinguished by wider separation of the spermathecal pores, possibly also by presence of hearts in xiii and of a pair of female pores. Paired female pores are unknown in Indian species except after head regeneration and the genus is defined as having an unpaired pore. Hearts originally were said to be present in xiii but subsequent dissection of another specimen found last hearts in xii. Variation in location of latero-esophageal hearts is very rare in *Perionyx,* except after cephalic regeneration when it may be considerable, depending on level of regeneration, condition of specimen, etc. Other fragments of information (unfortunately too few though a number of specimens were available for study) also hint at a possibility of regeneration. Closer relationships may well prove to be with undescribed Burmese species unfortunately never obtained at a mature enough stage to warrant erection of new species.

Many hundreds of perionyxes were collected at various occasions over a period of years in the Toungoo Karen Hills in vain attempts to obtain further adults of *ditheca* and of *arboricola*

Rosa, 1890 (known only from a clitellate type found more than seventy years ago). Many thousands of perionyxes from other parts of Burma, secured during the season when most earthworms breed, also were too immature to warrant specific identification. In India, many hundreds of individuals were dug up from one site at irregular intervals during a period of more than a year in a futile attempt to obtain normal clitellate specimens of *millardi* (also cf. *P. simlaensis* below).

Clitellar tumescence of worms kept in the laboratory remained maximal (with occlusion of dorsal pores and obliteration of intersegmental furrows) only for a short period. Before long the clitellum disappeared when its site could be recognized only by color differences from adjacent regions, whiteness or a distinctly different shade of red. The literature provides good reasons for believing that few if any of the types of oriental species had a clitellum in maximal tumescence. Many may have been in a presexual stage (at which mature sperm often are recognizable on male funnels) or in a postsexual stage (at which spermatozoal iridescence usually is unrecognizable on male funnels and in spermathecae). At least 6 oriental species of *Perionyx* were erected on admittedly aclitellate specimens and just how juvenile some of them may have been is unknown — types of *dubius* were so young that spermathecae had not yet grown into coelomic cavities. Presumably then, maximal clitellar tumescence is attained rather quickly after which breeding soon is finished and then is followed by rapid regression of the clitellum. If sexual period is correlated with the monsoon cycle as in most oriental earthworms, it almost certainly is not, at least in Burma, earlier than in other genera.

PERIONYX EXCAVATUS Perrier, 1872

India

Pulta Waterworks, near bungalow, 0-0-1. Pulta Waterworks Survey. (Indian Mus.)

Pushok, hillsides near bungalow, December 1926, 0-0-82. S. L. Hora (Indian Mus.)

Gauhati, Assam, compound of Cotton College, March 1942, 0-0-2. P. K. Das.

Dehra Dun, United Provinces, October, 78-4-22. M. Matthur.

Almora, United Provinces, in wet ground near spring, at elevation of *ca.* 6000 feet, June, 0-0-15.

Philippine Islands

Manila, Sampaloc, garden, September 1958, 0-0-2. Magdalina Cantoria per Y. Kondo.

Fiji Islands

Suva, January 25, 1939, 0-0-1. Tree hole, May 20, 1945, 4-0-0. R. A. Lever per N. Tebble.

Tailevu, January 21, 1946, 0-2-0. R. A. Lever per N. Tebble.

Levuka, Ovalau, banana stem, November 12, 1945, 1-0-0. R. A. Lever per N. Tebble.

Hawaii

Honolulu. Semi-damp soil covered with plant debris and some animal faeces, dairy farm, University of Hawaii, May 23, 1956, 0-0-2. Very wet soil saturated with animal faeces along drainage canal, dairy farm, University of Hawaii, May 23, 1956, 1-1-14. J. E. Alicata.

Manoa Valley, Oahu, humus, banana plantation, March 8, 1959, 1-0-0. Y. Kondo.

External characteristics. Segments, in specimens without indications of posterior amputation or regeneration, 123, 128, 129 (small juvenile), 131 (2 specimens), 139, 140, 143, 145, 146, 147, 152, 153. Pigmentation red, restricted to dorsum except in front of clitellum where ventrum is invaded and increasingly so towards anterior end. Prostomium epilobous, tongue open. Nephropores, never obvious and often unrecognizable, near mL and close to margin of pigmentation, in a rather irregular rank on each side of body.

Male pores lateral and very slightly anterior to penial setae, usually recognizable only after removal of cuticle and when traction on the epidermis has separated the lips. Each pore, and its adjacent group of penial setae, is in a transversely elliptical white area, usually more or less raised and with a slight transverse cleft in which the tips of 4-9 penial setae are just barely distinguishable. The two rather indistinctly demarcated elevations do not quite meet at mV and are included in a common male field with a fairly distinct boundary anteriorly and posteriorly but not laterally. The field (except for the white areas) usually is greyish translucent and slightly depressed but occasionally is quite level or even slightly protuberant.

Internal anatomy. Pigment, associated with circular muscle layer except in preclitellar segments of very dark individuals in which considerable pigment is deposited in an outer portion of the longitudinal layer, lacking just underneath the intersegmental furrows and very sparse for a short distance on each side. No trace of the alternation of transverse bands of dense and sparse deposition that is obvious after removal of the longitudinal musculature is recognizable externally. Special longitudinal muscle band at mD usually densely pigmented. Septa are delicate, without marked muscularity. More or less obvious peripheral thickenings, without characteristic shape, of several to a larger number of consecutive septa beginning in the region from 15/16 to 20/21, have been noted in a number of specimens. The degree of thickening varies considerably.

Esophagus very vascular in x-xii or xiii, widened and bead-shaped in xiii, with fairly high irregular longitudinal ridges on inner wall in xi-xiii or xiv, valvular in xv. Typhlosole lacking. (Intestinal origin in xv and/or xvi?)

Dorsal blood vessel, single throughout, complete, bifurcates under the brain, the two branches reuniting above the subpharyngeal ganglion to become the ventral trunk. A supra-esophageal trunk is present in vii-xii, bifurcated posteriorly twice, one branch to the heart of xii, another passing through 12/13 to disappear into the anterior face of the esophageal widening in xiii. Subneural trunk, adherent to parietes, usually appears to turn laterally in xiv or xiii and then to pass onto gut in xiii to join an extra-esophageal. Extra-esophageal trunks, median to segmental loops of viii, pass onto gut about at level of 8/9 but do not unite mesially. One of them usually appears to pass off from the gut to the parietes and under the nerve cord into the subneural behind the seeming lateral bend of that trunk. Some portion of the subneural usually has blood and is quite obvious, but empty portions often are unrecognizable in field preserved material. Small vessels pass off from dorsal trunk in vi-ix, those of vii-ix at least joining the ventral trunk and hence known as lateral loops or hearts. Hearts of vi usually have been traceable to the ventral trunk. A pair has been found in v in two specimens only, in neither of which the vessels could be traced to the ventral trunk. Large hearts are present in x-xii with obvious blood-filled connections with the supra-esophageal but the branches to the dorsal trunk are without blood, filamentous or unrecognizable.

Nephridia avesiculate, rather small, ducts long and slender, passing into parietes in a slightly irregular rank on each side of body.

Male gonoducts, without epididymis, join ental ends of prostatic ducts. Seminal vesicles of xii are large and appear to extend through xiii or xiii-xiv but actually are confined to pockets of 12/13. One vesicle, usually that on the right side, is about a half or even less the size of the other. The vesicles are in contact dorsally though not in the median plane, but in spite of appearances never seem to be united. The vesicles of xi are partly or wholly surrounded by coagulum from which, in some field preserved material, they may not be distinguishable. The coelomic cavity of x also is filled with coagulum. The prostates are confined to xviii (noted in 50 specimens). The duct is embedded in the gland and an ental portion is sinuous or in one or two small loops. Penial setae have nine or more rather irregular circles of spines though these occasionally seem to be arranged in a spiral rather than in discrete circles.

Ovaries fan-shaped and sometimes folded like a fan, each with several to numerous egg strings. Spermathecae are of medium size and then reach up only to level of dorsal face of gut which is low or are large enough to nearly touch the dorsal parietes. The duct is shorter than the ampulla and has a fairly large lumen. Most of the sperm is present in club-shaped spermatophores that are thicker entally where the iridescence is centrally located. The narrowed portion is yellow, transparent, and this portion often is visible in an open spermathecal pore. The spermatophores are in the duct and an ectal portion of the ampulla. Small spaces in the wall of the duct near the ental end sometimes are recognizable. Presence usually is indicated by roughenings or protuberances of the outer surface that may have an appearance of clusters or of an annular band. One or two of the chambers may be enlarged and especially protuberant. Sperm sometimes has been found in the chambers.

Reproduction. Iridescence on male funnels usually is brilliant and indicative of profuse maturation of sperm. Iridescence is recognizable also in spermatophores (never found outside the spermathecae) as well as sometimes in the intramural chambers of the spermathecal duct. Reproduction, since sperm are matured and exchanged in copulation, is assumed to be sexual and biparental.

Spermatozoal iridescence is brilliant on male funnels of aclitellate individuals in which seminal vesicles had reached maximum size though spermathecal ampullae are undistended and prostates are not mature. Spermatozoa are lacking in the spermatheeae and evidence for copulation prior to development of the clitellum has not been found.

Regeneration. Posterior amputation is so common that determination of normal segment number is difficult. Half of the specimens in one series already had tail regenerates. Cephalic regenerates soon become indistinguishable from substrates except for the anomalies of internal structure that often result from epimorphosis and/or morphallaxis. The abnormalities of the two specimens described below probably arose in this way.

Abnormality. No. 1. All organs from spermathecae posteriorly, one segment in front of usual position. Presumably resulting from hypermeric regeneration (—1) at some level in front of the first spermathecal segment.

No. 2. Spermathecal pores at 8/9-9/10. Female pores in xv, xvi. Male pores in xix. Lateral hearts in vii-x. Latero-esophageal hearts in xi-xv. (Intestinal origin in xx?) Bead-shaped widening of esophagus in xvi. Testes and male funnels (with spermatozoal iridescence) in xi-xii. Seminal vesicles in xii-xiii. Ovaries in xiii, xiv and left side of xv. Gonoduct funnels in xiii of female size but with plications as in male funnels. Normal male funnels are present in both sides of xiv and xv. Male terminalia, in xix, normal. As in case of the first specimen none of the usual external indications of regeneration are recognizable. Hypermeric head regeneration (+1) presumably had been involved.

Remarks. An accurate characterization of two portions of the digestive system has not been achieved, in part perhaps because of condition of material and/or because of individual variation. A gizzard has seemed to be present in v or in vi, in about equal numbers of specimens, rarely in both v and vi and then with septum 5/6 apparently inserted about at its equator. A gizzard was not distinguishable, macroscopically, in other specimens. Intestinal origin doubtless is posteriorly in xv or anteriorly in xvi but insertion on gut of septum 15/16 was recorded in the laboratory notes as esophageal or intestinal for nearly equal numbers of dissections. Each of the above mentioned determinations was for a worm that could not be suspected of having regenerated, as gizzard location and intestinal origin often is variant after head regeneration.

The intestine often is narrowed in region of xvii-xviii, sometimes so much so that the portion in xviii appears to be valvular. Enlargement of the prostates as they become functional during the reproductive season presumably considerably compressed the gut. At greatest compression determination of intestinal origin becomes even more difficult.

A whitish deposit on the parietes in several worms from the western Himalayas sometimes was separated into small bits that looked superficially somewhat like micronephridia. Shreds of disintegrated peritoneum that remain attached to the muscular layer also sometimes look superficially like micronephridia.

Small protuberances sometimes seen on preseptal necks of nephridia in postclitellar segments may be adventitious or rudiments of secondary nephrostomes.

The subneural trunk or any portion thereof that is completely empty may be unrecognizable in dissections.

P. excavatus seems to be equally at home in the lowlands of tropical Burma and in the Himalayas at elevations up to 9000 feet. This is most unusual for an earthworm. Although the species has been widely transported, successful colonization now appears to be restricted to tropical lowlands, from Madagascar east to the Hawaiian Islands.

PERIONYX HORAI Stephenson, 1924

India

Cherrapunji, Assam, along stream, Munbow side, 0 0-1. (Indian Mus.)

External characteristics. Diameter, 4 mm. Setae, present from ii, more closely spaced in ventrum than in dorsum: 36/viii, 45/xii, 44/xx, vii, ix/3-4, lacking or invisible ventrally on viii. Clitellum (? indicated only by whitening of epidermis), annular, from 12/13 to 16/17, intersegmental furrows, dorsal pores and setae present.

Spermathecal pores, very small transverse slits, on 7/8-8/9. Female pore, presetal, median. Vestibular aperture open, slightly longer than wide. Intersegmental furrows 17/18 and 18/19 visible on anterior and posterior walls of vestibulum which is continued anteriorly and posteriorly above the furrows. Roof cross-hatched by slight furrows into rather small tumescences and with a deep longitudinal groove at mV. Penial bodies, just lateral to the groove, 1+ mm. long, bifurcated ventrally. A deep (seminal?) groove on lateral or anterolateral face of each penial body, continuous with a shallower branch along each terminal digitiform lobe, passes up onto vestibular roof and then anterolaterally. Male pores, presumably minute, closed and concealed by soil particles, were not found though prostatic duct was traced through parietes into anterior end of seminal groove.

Internal anatomy. Gizzard, wide, in v. Intestinal origin in xix (?), gut gradually attaining full width in xx-xxi.

Segment xi short, 10/11 and 11/12 held together by sticky coagulum so that the whole mass at first looked like a single muscular septum. Seminal vesicles of each pair united dorsally and hence horseshoe-shaped. Prostatic ducts, about 2 mm. long, an ental portion slender and u-shaped, ectal portion with muscular sheen and straight, passing into lateral face of vestibulum which is conspicuously protuberant into coelomic cavities of xvii-xix.

Spermathecal duct muscular, narrowed abruptly just at or within the parietes, with a short, thin-walled, non-muscular(?) neck entally. Lumen rather irregularly slit-like ectally due to presence of several high ridges, abruptly narrowed and eccentric entally, almost circular in section just below the neck where it is again widened. Seminal chambers very small, ovoidal to spheroidal and closely crowded in a nearly annular band (but with one fairly wide gap) around neck of duct. Six to eight apertures into duct lumen were found.

Reproduction. Spermatozoal iridescence was recognized in the seminal chambers. As sperm are matured and exchanged in copulation, reproduction is assumed to be biparental.

Remarks. The worm is strongly contracted and brittle.

The invagination containing the penial bodies is similar to that of certain species of *Eutyphoeus* and, as in those forms, is called a vestibulum.

The species has been known hitherto only from the original account of six aclitellate types. The gizzard was believed to be in vi. However, one of the two dissected worms was abnormal, possibly as a result of anterior regeneration. Aggregation of spermathecal seminal chambers into a single band rather than two rosettes does not, at present, appear to contra-indicate the identification.

The clitellum of the present specimen, which is from the type locality, very probably had not become especially tumescent though copulation obviously had taken place.

Spermathecal pores were at 7/8-8/9 in four of the types and that location was regarded as normal. Divergent locations in two specimens, at 6/7-7/8, and 8/9-9/10, could have resulted from cephalic regeneration. Data as to location of other organs in those two worms could confirm the inference and might enable good guesses at level of regeneration. Again, it was fortunate that the two aberrant worms were not the only ones secured. Percentage of homoeotic individuals (33⅓ per cent) is high.

P. horai appears to be close to *P. simlaensis* from which it is distinguished by a distal bifurcation of the penes, the intersegmental location of spermathecal pores and, possibly, by a more deeply invaginate vestibulum.

PERIONYX MODESTUS Stephenson, 1922

India

Dumpep, Khasi Hills, Assam, under stones on the dried up bank of Wasarah Stream, 31/3/30, 0-2-18 (poorly preserved). J. L. Bhaduri. (Indian Mus.)

Dumpep, 0-8-0. S. L. Hora. (Indian Mus.)

External characteristics. Length, 94-206 mm. Diameter, 3-6 mm. Segments, 170-220. Pigmentation, red, though dorsum appears blue. Nephropores, whenever recognizable, just above ventral limit of pigmentation. First dorsal pore at 3/4 (1 specimen), 4/5 (21, on 18 of which a more or less pore-like marking present at 3/4), 5/6 (1). Clitellum, presumably not fully developed, indicated only by a slight reddening or whitening of the epidermis between 12/13 and 16/17. Setal formulae, as indicated below; no penial setae nor are any setae present between male pores ventrally.

TABLE 1

Setal formulae of *Perionyx modestus*

					viii/	xix/	
44	44	42g	49	g	5g	6	First lot
46	44	49	50	48	11	10	
42	56	51	49	g	12	7	
41	43	36g	52	47	1g	8	
43	43	56	51	45	12	11	
40	45	49	51	49	15	8	Second lot
31	47	52	50	52	18	9	
43	45	56	56	48	16	6	
63	68	84a	60	54	16	7	
38	48	45	45g	44	14	7	
/ii	/iii	/viii	/xii	/xx			

g, gaps in setal, circle, follicle apertures recognizable or invisible.
a, setae, on this worm, unusually closely crowded dorsally.

Spermathecal pores not closely paired; each may have a protuberant and annular lip. Female pore presetal and median.

Male field usually transversely, occasionally longitudinally, elliptical, dislocating 17/18 anteriorly and 18/19 posteriorly, extending laterally into region of *FI*, definitely delimited by a slight furrow, flat and slightly raised, slightly or deeply depressed, occasionally especially so at mV. A transverse equatorial groove is deepened laterally and there contains, on each side, a short penis circular to elliptical in cross section, with the minute male pore on the flattened ventral end. These penes may be so deeply retracted as to be invisible even after separating margins of the groove and then can be found only by slitting open the prostatic duct. A penis (of one worm) is protuberant from center of each of two longitudinal cushions that are on the sides of an especially deep median depression of the male field. One cushion is transverse and with a ventral transverse slit on a worm that has no recognizable trace of cushion or penis on the other side. Setae and follicle apertures, quite unrecognizable midventrally between the penis, first visible laterally just at margins of the field.

Internal anatomy. Gizzard in v (9 specimens), however 5/6 appears to be (three worms) inserted at or near the equator so that the posterior half or less seems to be in vi. Intestinal origin apparently in xix (3) or xx (2). Circulatory system as in *P. miniata* Gates, 1945, except that the last hearts are in xiii (12 specimens).

Male funnels large, sometimes reaching nearly to level of dorsal surface of gut. Seminal vesicles, in both xi and xii, usually united above the gut and horseshoe-shaped. Prostates confined to xviii, ducts 4-6 mm. long, each usually in a U-shaped loop, with ental limb slender and white, ectal limb thicker and with muscular sheen.

Spermathecae, large, reaching into contact with dorsal parietes. Duct much narrower and shorter than ampulla, probably slightly muscular, not specially narrowed within the parietes but abruptly narrowed entally, with a transversely slit-like lumen. Surrounding the neck portion is a collar of small chambers. This can be removed, in some worms, without apparent damage to duct. The apertures into seminal chambers then seem to be on a thickening of the floor of the ampulla and in a circle around the larger opening of the ampulla into the duct (a result of some unusual relaxation or distention of entalmost portion of duct?). Seminal chambers, in other worms, open into the ectalmost portion of the neck. Spermatozoal iridescence has not been recognized within any of the supposed seminal chambers though strands of very sticky, slightly iridescent material pass to the apertures.

Reproduction. Sperm are matured and exchanged in copulation. Hence, reproduction is assumed to be biparental.

Abnormality. Several specimens were homoeotic. At the middle of an uninterrupted gonad sequence, in one of the worms, there was a testis and male funnel on one side of the segment, an ovary and female funnel on the other side. The number of gonads, in each homoeotic, was greater than normal and the sequence was uninterrupted. Gonad ratios (testes:ovaries) were: 2:8, 4:4, 4:6. Ratio in normal specimens, in all species of the genus with but two exceptions, 4:2 (testes and ovaries separated by an agonadal segment). In regenerated heads, ovaries very often are more numerous than in normal and unregenerate worms. Internal organization of the Assam worms showed that the homeosis originated after hatching and during regeneration of a lost anterior portion.

Regeneration. Organization of the homoeotics permits the following conclusions. Anterior regeneration in *P. modestus* is possible, and can be equimeric, at all levels back to 15/16 at least. All reproductive organs of the pre-intestinal region of the body, i.e., all except the male terminalia, develop, in appropriate conditions, in homomorphic head regenerates. In species with that much regenerative capacity, head regeneration is possible back into the last quarter of the body and can be expected in *modestus.*

A tail regenerate 13 mm. long is present on a 70 mm. substrate. The two larger specimens have tail regenerates, and other large worms are posterior amputees.

Parasites. Nematodes are present in coelomic cavities of x in two worms.

Remarks. This species has been known only from the original account of types that were not clitellate. Smaller ones, *ca.* 85 mm. long, were said to be sexual and if so may have been of the same species as the larger and more immature ones. If, however, worms were juvenile, taxonomically important characters might not have been recognizable. Aside from the smallness of the (juvenile?) spermathecae, the only important differences from present material are absence of penes (unrecognized because of deep retractions?), and absence of a collar of seminal chambers (also unrecognized or unrecognizable because not yet developed) on the spermathecal duct.

Perionyx simlaensis (Michaelsen, 1907)

India

Saharanpur, United Provinces, October, 58 small juvenile, 477 medium to large juvenile, 11 early aclitellate, 2 clitellate and 4 postsexual aclitellate specimens. M. Mathur.

External characteristics. Length (strongly contracted) to 160 mm. Diameter (clitellate specimens which are slenderer than the larger juveniles) to 6.5 mm. Segments to 200. Pigmented, dorsum red but often apparently dark blue anteriorly. Prostomium, epilobous, tongue open (34 specimens), apparently closed (1). First dorsal pore, at 4/5 (34), 5/6 (1). Setae, present from ii, more closely spaced ventrally than dorsally, no definite middorsal or midventral gaps in the circles. Setal formula of the largest juvenile, 63/ii, 64/iii, 50/viii, 53/xii, 53/xx. In large juveniles and more mature specimens, viii/5-8, xvii/4-7, xviii/0-1, xix/4-7. Small juveniles usually have 1-5 setae between rudiments of male pores, 1 (4 specimens), 2 (5), 3 (10), 4 (8), 5 (1). The setal circle is unbroken ventrally in the smallest juveniles and rudiments of male pores are quite unrecognizable. Nephropores, in somewhat irregular longitudinal ranks.

Spermathecal pores, minute, in longitudinal grooves extending back from 7/8 and 8/9 into viii and ix. Female pore definitely single and median (1 specimen) and probably one other, paired pores possibly present (1), unrecognizable on the others. Male pores, presumably minute, but not recognized. Male field as in Michaelsen's specimens except that cushions bearing the penes may be on lateral walls of a deep depression having a transversely rectangular aperture, the cushions nearly in contact mesially.

Internal anatomy. Pigment, red, present in both circular and longitudinal muscle layers, density markedly decreasing posteriorly in the longitudinal layer.

Gizzard, rather small, in v (20 specimens). Gut widened in xiii-xvi, with fairly well developed calciferous lamellae in xiv-xv, less well developed in xiii and in xvi, numerous small calcareous granules still present between lamellae of xiv-xvi or (incomplete clitellate worm) xiv-xvii, when worms were dissected several weeks after preservation. Intestinal origin in xviii (5), xix (14), xx (2, including the incomplete clitellate). No typhlosole (20). The portion of the gut in xvii may be valvular or with low lamellae continued from xvi (especially in worm with intestinal origin in xx). The gut wall in ix or x-xiii is heavily vascularized.

Dorsal blood vessel, single throughout, bifurcates underneath the brain, the branches reuniting ventrally to form the ventral trunk. A small median branch may be recognizable above the brain. The subneural trunk is continued anteriorly to the region of the subpharyngeal ganglia where it bifurcates. A large branch passes off to right or left side in xiv or xv and in xiii becomes continuous with one of the extra-esophageals which of course are median to the hearts as they pass onto ventral surface of gut in x. Hearts of x-xiii latero-esophageal, the last pair in xiii (20). Hearts or segmental commissures of ix-viii are lateral. Commissures of v-vii may pass to the ventral vessel on one side or the other. Three pairs of vessels from the ventral trunk are recognizable between 4/5 and the anterior bifurcation. Nephridia avesiculate and, relative to size of body, rather small.

Holandric, the testicular coagulum of x usually, that of xi occasionally, appears to be within a cylindrical testis sac but the membrane covering the coagulum may be only loosened peritoneum. Seminal vesicles in xi and xii only (20 specimens). Prostates confined to xviii (20). Prostatic duct rather short, stoutish, bent into two u-shaped loops. Male gonoducts pass through the anterior portion of the gland to open into the ental end of the prostatic duct. No penial setae.

Abnormality. (No. 1) Spiral metamerism involving ii-v. (No. 2) Spiral metamerism involving xv-xvii. (No. 3) Spiral in middle of body, involving 31 segments, none of the abnormality recognizable ventrally. Other specimens may have had spiral or other metameric abnormalities in a postclitellar portion of the body as no attempt was made to check metamerism in that region. (Metamerism always has been checked, for many years, in an anterior portion of the body back at least to male pores or to clitellum if that is more posterior.)

(No. 4) First dorsal pore at 5/6. Spermathecal pores at 8/9-9/10. Female pore in xv. Male pores in xviii. Gizzard in vi, calciferous lamellae in xv-xvii, intestinal origin in xx, last hearts in xiv. Small male funnel in xi on left side, testes and male funnels in xii-xiii, seminal vesicles in xiii-xiv, ovaries and female funnels in xiv. Prostates large but confined to xviii. Aclitellate.

(No. 5) First dorsal pore at 5/6. Spermathecal pores at 7/8-9/10. Female pores in xiv-xv. Male pores in xix. Segment xvi incompletely separated from xv on the right side, setal circle of xvi on that side represented only by a few scattered setae. Septum 15/16 lacking on right side though nephridia of xv and xvi are present on both sides. Gizzard in vi, calcareous granules between lamellae of xiv-xvii, esophageal valve in xviii-xix, intestinal origin in xx, last heart in xiv on left side. Testes and male funnels in xi-xii, seminal vesicles in xii-xiii, ovaries in xiii and left side of xiv. Aclitellate.

(No. 6) First dorsal pore at 5/6. Spermathecal pores at L7/8, 8/9-9/10, L10/11. Clitellum on xii-xviii. Female pore in xvi. Male pores in xx. Spiral abnormality involving xiii-xvii but invisible ventrally where segments were counted. Gizzard lacking. Testes and male funnels in xii, a rudimentary male funnel in xi, seminal vesicles in xiii, prostates in xviii if counted on right side, xix if counted on the left. Intestinal origin apparently behind the prostates? Ovary and oviducal funnel of left side one segment anterior to those of the right side.

Regeneration. Anterior amputees and recent anterior regenerates were found only among the medium to large juveniles in which group 3.7 per cent of the individuals had been affected. All anterior (as well as the posterior) regenerates were exactly at intersegmental levels. Number of segments in metamerically differentiated purely cephalic regenerates: 7 at 7/8 (2 regenerates), 8 at 9/10 (also with a tail regenerate at 74/75), 10 at 10/11, 11 at 11/12 (tail regenerate at 114/115), 16 at 15/16, 16 at 16/17 (tail regenerate at 142/143), 17 at some level behind xviii (2 regenerates one of which probably was far behind xviii). Segment size in some of these regenerates already was the same as in unregenerate worms of similar thickness and age. Though regenerative growth apparently had been completed, pigmentation still was clearly distinguishable from that of the substrate. Older cephalic regenerates, in absence of external or internal evidence of homoeosis or organ multiplication, would have been unrecognized.

One unusually interesting anterior regenerate (S-4) was mainly cephalic and normal except for presence on the ventral side slightly left of the median line of a white tubercle bearing a slit-like aperture. The latter opened by a slender passage through the pharyngeal floor into lumen of regenerate gut which lacked a gizzard. The substrate, in this case, was a 43-segment fragment which appeared from its size, pigmentation and segmental characteristics to have been excised from a region well within the last quarter of the body, perhaps behind 150/151. The anal tubercle is the last vestige remaining from regularization of a regenerate that originally was a heteromorphic tail. A short and normal tail regenerate posteriorly also was present.

Many of the worms, prior to collection, had lost a posterior portion of the body: 31 per cent of the small juveniles, 28.7 per cent of the medium to large juveniles, 36.3 per cent of presexual aclitellates, 50 per cent of the clitellates, 100 per cent of the postsexual aclitellates. Healing of unregenerate worms sometimes had been enteroparietal but in many cases, especially at more anterior levels, an appearance of such healing was provided by median contact of margins of the last segment in such a way as to simulate a vertically placed anal aperture. Separations of those margins revealed a slightly depressed, circular cicatrix which was either quite imperforate or centrally punctured by a pin-point-like opening through apposed gut wall and thin cicatrix. Homomorphic tail regeneration obviously is possible (cf. Table 2) at any level behind 27/28. Two worms showed consecutive tail regeneration, at 52/53 and 75/76, at 66/67 and 106/107. Three distinct shades or grades of pigmentation were recognizable on each specimen, changing from one type to another at an intersegmental furrow. As other external stigmata of regeneration had disappeared even the most recent regenerates must have been old.

Reproduction. Biparental reproduction is assumed. Copulation and cocoon deposition may be limited to a short period at end of the monsoon rains. If so, two years may be required for attainment of sexual maturity, the dry periods being spent in some sort of a diapause. Evidence provided by specimens secured at end of the period of activity indicates that neither cephalic nor caudal regeneration is restricted to diapause or seasons of inactivity.

Remarks. Live specimens naturally relaxed can be expected to reach a length of more than 300 mm.

A male field is quite undemarcated in a very large majority of the specimens. A shallow transverse groove often is visible ventrally at eq/xviii. A slight depression at each end of the groove presumably marks sites of male pores between which, and in the groove, tips of 1-3 setae usually are visible. The male field, at that stage of development, appears to be about as in the types of *P. modestus*.

Seminal vesicles were lacking in ix-x of all normal individuals. Coagulum in x may have been mistaken for vesicles but what could have been mistaken for vesicles in ix? Nothing else in the description of the types suggests abnormality.

One clitellate Saharanpur specimen is abnormal in the cephalic region. The head of the other was lost near 13/14 at time of collection. Four of the presexual aclitellates, those with best development of the male field, are abnormal. How much regression of sex organs there may have been in the postsexual aclitellates could not be determined. In these circumstances characterization of spermathecae and of male terminalia (especially with reference to presence or absence of a vestibulum) is inadvisable.

The description above is based on supposedly normal specimens. More variation is indicated in segment of intestinal origin and in the extent of a valvular portion of the esophagus, than, for instance, in most species of *Pheretima*. Nevertheless, it must be remembered that some of the supposedly normal large juveniles could have regenerated so long before collection and in such a manner that no indication of regeneration would have been recognized. While fasting, especially during regeneration more anteriorly, one or more segments at the beginning of the intestine sometimes become narrowed so much as to be externally undistinguishable from a contracted valve. Possibly histological differences can be found but microtome sectioning was not possible when the material was available.

P. simlaensis certainly appears at present to be very close to *P. horai*. Aside from the genitalia, closely related species are most likely to be distinguishable from each other by size, color, number of segments, pattern of pigment deposition and minor characters of that sort. Yet norms for most of those characters in a local population could not be determined even from a sample of 500 odd specimens. In a genus with such an unusually high regenerative capacity as *Perionyx* at least some knowledge of that capacity should be helpful in estimation of species norms and relationships, especially when a very few specimens of a supposedly new species are available. Epimorphosis in combination with morphallaxis certainly provides a vast variety of organization some of which, it is hoped, will be recorded in a future publication.

TABLE 2

Levels of posterior regeneration in one collection of *Perionyx simlaensis*

27/28	1 specimen	95/96-99/100	8
35/36-39/40	1	100/101-104/105	4
40/41-44/45	6 specimens	105/106-109/110	5
45/46-49/50	2	110/111-114/115	4
50/51-54/55	4	115/116-119/120	3
55/56-59/60	6	120/121-124/125	4
60/61-64/65	5	125/126-129/130	6
65/66-69/70	4	130/131-134/135	5
70/71-74/75	6	135/136-139/140	7
75/76-79/80	2	140/141-144/145	3
80/81-84/85	8	145/146-149/150	3
85/86-89/90	4	150/151-154/155	3
90/91-94/95	13	155/156-159/160	2
		160/161	1

Genus WOODWARDIELLA Stephenson, 1931

By definition, this classical genus is ''purely meganephridial.'' In more modern terminology the excretory system is holonephridial or holonephric, each of the anlage in a pair of embryonic somites having developed into a single nephridium with a preseptal funnel, a postseptal looped body, and an external aperture in the epidermis of the metamere containing the postseptal portion. Typically, a pair of such nephridia (and no others) is present in each segment except the first and last. Interpretation of ''nephridial tufts,'' when scattered micronephridia were absent (or perhaps only unrecognized because of minute size or poor preservation), as meganephridia, in the classical system, required inclusion of several small oriental species in the Australian *Woodwardiella*. One of those species, *bahli* (Stephenson, 1925) subsequently became the type of *Nellogaster* which is related to *Lampito*. Another species, *burkilli* (Michaelsen, 1907), went into *Nelloscolex* which is related to *Tonoscolex*. These four genera, though as yet little known and incompletely characterized are modern rather than neoclassical, being defined, insofar as circumstances permitted, in accordance with new insights as to evolutionary conservatism and plasticity of somatic and genital systems in earthworms. (A genus, originally classical but now defined more adequately in the modern manner, is *Eutyphoeus* — *vide* Gates, 1959.)

Supposedly meganephridial tufts of *W. pumila* were found (Bahl, 1942) to be clusters of discrete micronephridia. The species, as then characterized, clearly did not belong in any of the modern genera and so had to go, in the unrevised major portion of the classical system, into *Notoscolex*. Excretory systems of the remaining oriental species of *Woodwardiella* still are as inadequately characterized as those of *bahli* and *pumila* originally were but presumably are meronephric regardless of size of nephridial tubules. (Meganephric is not synonymous with holonephric as meronephric systems may have one to several pairs of meganephridia, usually in addition to the more or less numerous micronephridia.) Accordingly, *W. hastata* (Stephenson, 1915) *sarasinorum* (Michaelsen, 1897), *uzeli* (Michaelsen, 1903), and *kayankulamensis* Aiyer, 1929, are now transferred to *Notoscolex*, primarily to avoid necessity of considering an Australian genus in future discussion of geographical relationships of oriental earthworms.

Genus NOTOSCOLEX Fletcher, 1886

The digestive system in this classical genus, without reference to caeca, typhlosoles and supra-intestinal glands, would have to be characterized as follows: Gizzard in v or vi. Calciferous glands (omitting any mention of structure) lacking or: one pair in xvi or xv-xvi or xv-xvii, two pairs in xi-xii or xiv-xv, or xiv-xvi, three pairs in xiv-xvi or xv-xvii, four pairs in x-xiii, five pairs in ix-xiii, six pairs in viii-xiii, etc. Intestinal origin in xv, xvi, xvii, xviii or xix. Little is known even about the major trunks of the vascular system. The excretory system, by definition, is required only to be micronephridial. All species probably are meronephric but some are "purely micronephridial." In others "various combinations of mega- and micronephridia" have been recorded. Furthermore, prostates are of at least two sorts: 1) Tubular (though with slight lateral branchings of the central duct that may be recognizable only in microtome sections) and presumably of ectodermal origin. 2) Racemose, of the pheretima sort and then presumably of mesoblastic origin. Distribution, omitting mention of isolated areas where introduced forms now are domiciled, Australia and New Zealand, South India and Ceylon.

Such a congeries has no geographical justification and obviously is not based on the over-all similarity that is to be expected in species so closely related as to belong together in one genus.

The type species of *Notoscolex*, *N. camdenensis* Fletcher, 1886, is Australian. Though inadequately characterized for present needs, it is generically distinguishable from *pumila*. For the latter a new genus now is erected.

LENNOSCOLEX gen. nov.

Setae four pairs per segment, *d* gradually becoming more dorsal posteriorly, *a* and *b* of xviii penial (or lacking?). Quadrithecal, pores on 7/8-8/9. Female pore median and slightly pre-equatorial, on xiv. Male pores, common apertures of prostatic ducts and penisetal follicles, on xviii. Clitellum annular, dorsal pores occluded, intersegmental furrows obliterated, setae retained, on xiv-xvii at least. (Pigment lacking.)

Septa all present from 5/6. Digestive system with one esophageal gizzard in v, intestinal origin behind xv, without calciferous glands, caeca, typhlosoles and supra-intestinal glands. Vascular system with unpaired, complete dorsal and ventral trunks, paired extra-esophageals median to the hearts, a supra-esophageal trunk but no subneural (instead, a pair of posterior latero-parietal trunks?), and latero-esophageal hearts in x-xii or xiii. Excretory system meronephric and without nephrostomes, behind the clitellum with one pair per segment of clusters of four to six small exonephric nephridia. Holandric, seminal vesicles in xi-xiii. Prostates racemose, of pheretima sort, the ducts joined entally (?) by the vasa deferentia.

Type species. *Woodwardiella pumila* Stephenson, 1931.

Distribution. Presumably South India (Travancore and Cochin only?). Transportation responsible for domicile in Burma and Java.

Remarks. Definition is, of course, tentative.

Notoscolex minimus, peermadensis, kayankulamensis, travancorensis, all of Aiyer, 1929 and *tenmalai* (Michaelsen, 1910) appear to be candidates for inclusion in the genus.

The digestive system, except for the extension of the esophagus posteriorly, is very simple, perhaps primitive but the meronephry of the excretory system is very advanced.

LENNOSCOLEX PUMILA (Stephenson, 1931)

Burma

Ye, (Amherst), 0-0-2. K. John.

Bassein, September, 0-19-84. K. John.

Rangoon (Hanthawaddy), January 1931, 0-0-20, Various dates, 0-12-24. In marshy area across road from Cushing High School, 0-47-105. K. John.

Pegu, 0-0-2. K. John.

Regeneration. A young tail regenerate with dorsoterminal anus is present (1 specimen) at 78/79.

Remarks. Length of Rangoon worms, 70-90 mm., is unusual and may be due to relaxation during preservation or to softening during the period the worms have been in formalin.

Although all of the nephridia appear to have been characterized as ''integumentary'' and exonephric (Bahl, 1942, p. 34), the first of those two adjectives certainly seems inapplicable, at least to the preclitellar tufts which are located on anterior faces of septa and above the parietes. Some of such clusters, especially those of v-vi, when material in much better condition becomes available, may even prove to be enteronephric and with ducts opening into the pharynx.

Certain septal cell masses, one or two near each nephridial cluster of posterior segments, were thought (Bahl, 1942, p. 33) to be vestigial nephridia. If Bahl's assumption proves to be correct, the vestiges presumably would have been derived by longitudinal splitting in each of the two segmental anlage, such as is believed to produce the meromeganephridia of giant perionyxes in the Himalayas. Abortion of connections to the septa along with the preseptal necks and nephrostomes would then give the astomate condition prevailing in *pumila.* That astomate meronephry, regardless of method of evolution, now appears too highly specialized and possibly too nearly terminal to be in a direct line of ancestry to *Megascolex* and subsequently to *Pheretima,* even if there were no geographical contraindications.

Relationships now in need of investigation appear to be those of *pumila* with *N. minimus, peermadensis* and *kayankulamensis.* From *peermadensis, pumila* is distinguishable at present only by penisetal characters of unknown significance. Similarities of the Burmese worms to *kayankulamensis* already have been mentioned (Gates, 1942, p. 117). The excretory system of the Travancore species was thought by its author to be like that of

N. bahli. It is most regrettable that Bahl did not find opportunity to study these dubious species. All of the author's attempts to obtain collections of the Indian forms have been unsuccessful.

LENNOSCOLEX JAVANICA (Michaelsen, 1910)

The excretory system of this species never did get the requested characterization by Bahl. However, the anatomy as now known, is so like that of *pumila* as to make a transfer to the same genus seem advisable.

Like *pumila*, *javanica* obviously is exotic in Burma where it was introduced presumably quite recently and by man. Inclusion in *Lennoscolex* requires origin in South India (and perhaps Ceylon) where it has not yet been recognized.

Genus LAMPITO Kinberg, 1867

Studies of three somatic systems, digestive, vascular and excretory, in a peregrine species, enabled resurrection of this genus from the synonymy of the polyphyletic *Megascolex* and characterization more in accordance with modern requirements. Unfortunately, nothing has been learned since the genus was reinstated (Gates, 1938) about the endemic species, and various deductions as to overall similarity still require confirmation. Such data as were available, however, indicated evolutionary conservatism of somatic anatomy and greater plasticity of the genitalia. *Lampito*, in its various setal arrangements, shows that "a definite and natural line of demarcation in an evolutionary process" can constitute an arbitrary and unnatural taxonomic boundary unless all structure is taken into consideration to estimate overall similarity.

LAMPITO MAURITII Kinberg, 1867

Anadaman Islands

Haddo, January 1932, 21-4-2 and 3 fragments. (Indian Mus.)
Pahargaon, January 1932, 16-13-5, and some pieces. (Indian Mus.)
Aberdeen, Port Blair, South Andaman, May 1932, 12-3-5. (Indian Mus.)
Andaman Islands, September 1932-May 1933, 2-7-0. H. S. Rao. (Indian Mus.)

India

Nellore, Madras Presidency, September 7-10, 400-0-229. Helen Benjamin.
Udayagiri, Madras Presidency, September 11, 0-0-58. Helen Benjamin.
Kurnool, Madras Presidency, September 23-25, 139-53-64. W. D. Sutton.
Madras, December, 0-32-36. Dorothy Pearson.
Cuttack, Orissa, February, 0-9-14. H. S. Chaudhry.

Philippine Islands

Bataan, Luzon, 0-0-32. Leon Laplaize. (Eisen Collection, California Acad. Sci.)
Calayan Island, from ploughed field, 4(+)-1-0. (Eisen Collection, U. S. Natl. Mus.)
Pandacan, Manila, hog lots, Bureau of Animal Industry, 1954, 0-0-4. 1956, 0-0-2. P. Refuerzo.

New Caledonia

Tinchialit, at 2020 feet, October 1949, 0-0-1. L. E. Cheeseman per N. Tebble.

A single and median female pore is present on a number of specimens.

Pigment is present in the special longitudinal muscle band at mD. Extra-esophageal trunks, in some of the worms, are free from the gut all the way back through xii. Brain, connectives and subpharyngeal ganglia left in iii (2 specimens, once well forward), in iv (once) and then posteriorly, by a transverse section exactly along 3/4.

Ovaries, fan-shaped, with numerous egg strings which may have as many as eight ova. Ovisacs, small, acinous, with several ova.

Reproduction. Spermatozoal iridescence on male funnels and in spermathecae of most clitellate specimens indicated that sperm had been matured and exchanged in copulation. Reproduction accordingly is assumed to be sexual and biparental.

Abnormality. (Specimen No. 1) An extra small, atypical male porophore present on left side of xix. A penisetal follicle with setae but no prostate or duct is present in left side of xix. Two unidiverticulate spermathecae on the left side of ix are bound together by connective tissue. The right spermatheca of ix also has but one diverticulum which is anterior and bifid distally, as is the single diverticulum of the left spermatheca in vii. (No. 2) Two spermathecae on the right side of ix, the median of which has but one diverticulum and that on the median side. (No. 3.) Spermathecae of vii lacking. (No. 4) Two spermathecae on the right side of vii, each with a single anterior diverticulum. (No. 5) Spermathecae lacking on left side of vii but two present on the right side. The median spermatheca has a single anterior diverticulum slightly bifid distally. (No. 6) Spermatheca of left side of ix lacking, the spermatheca of the right side with only one diverticulum and that anterior. (No. 7) Spermathecal pore, on left side, at 8/9. Female pores on xv. Male pores on xix. Gizzard in v or vi (?). Intestinal origin in xvi. Last hearts in xiv. Testes and male funnels in xi-xii. Seminal vesicles in (xii?)xiii. Prostates in xix. Ovaries in xiv. The spermatheca has a lateral diverticulum only. A long series of metameric abnormalities, including helicometameres, is present from xxvi posteriorly but none were recognized anteriorly. The homoeosis of this worm probably resulted from hypermeric regeneration (+1) at or in front of 10/11. (No. 8) Extensive series of spiral metamerisms beginning with xvii. (No. 9-11) Each has a helicometamere, unrecognizable ventrally, involving ix-xii. (No. 12) Quadrithecal, pores at 8/9, left side of 7/8, and in an equatorial groove on the right side of vii. Intersegmental furrows and metamerism apparently normal except as now noted. Setae, except for *a*, are lacking on the right side of vii, and on the right side of vi only *a-d*, *f* and *h* are present. At equator of vii, on the right side, a groove is present that looks much like an intersegmental groove. Slightly behind *f* on the right side of vi is a short, slight but definite transverse furrow which contains no pore. Stigmata of regeneration are unrecognizable but in various species usually do disappear shortly in head regenerates. Amputation presumably was in region of 6/7 and somewhat irregular so as to result in loss of the left anterior spermatheca and perhaps a major coelomic portion of the right one. During regeneration there was some elongation of the substrate behind the level of amputation. Then new intersegmental furrows were formed across the elongated region. Such portion of the right anterior spermatheca as had escaped amputation had been almost completely histolyzed but the right middle spermatheca originally in viii and now opening to the exterior through an equatorial pore in vii had undergone no recognizable change during its migration.

Remarks. Pahargaon juveniles are all small and presumably had been hatched shortly before preservation.

L. mauritii obviously is exotic in the Andaman Islands as also in Burma. The original home of the species doubtless is in a southern part of the Indian peninsula from which worms have been frequently and widely exported. Successful colonization appears to have been limited to tropical lowlands.

Genus PHERETIMA Kinberg 1867

Generic definitions in the classical system, like those of families, sometimes contain descriptive matter indicative only of range of variation as known before 1900. Such statements, of course, should have been recognized to be liable to continual change as new species are found. One example is provided by the characterization of spermathecal pores in the classical definition of *Pheretima* (cf. Gates, 1959, p. 238) which was taken up into the subfamily definition. Omitting further consideration of descriptive text, the classical *Pheretima*, in effect, was defined as follows: Setae, perichaetin. Gizzard, between 7/8 and 10/11. Micronephridial. Testes and male funnels enclosed in testis sacs. Prostates, racemose. The last character is uniquely diagnostic of the family to which the genus belongs. The gizzard character is imprecise. Micronephridial, however defined, can have little significance at any hierarchical level of taxonomy. Testis sacs, even testes and funnels, are lacking in some morphs of certain species. Surely, more anatomical uniformity than that ought to be expected in species so closely related as to belong together in a good genus.

The reproductive, of all systems, is by far the best known in all earthworm families. It also is the one most affected by intrageneric evolutionary changes. New, macroscopically recognizable, genital, characters-in-common are unlikely to be found in a genus as large as *Pheretima*. They must be sought in somatic systems.

Two digestive organs usually were mentioned by most authors in species descriptions. The gizzard often was said to be in ix, ix-x or even x which, in spite of appearances, is morphologically incorrect. Septum 7/8 always is present and inserted on the esophagus in front of the gizzard. Whenever septum 8/9 is complete it is inserted on the esophagus just behind the gizzard. If 8/9, 8/9-9/10, or even 8/9-10/11 are abortive segmental vessels from the dorsal trunk usually show that the gizzard developed in the portion of the esophagus belonging to viii. Presence or absence of intestinal caeca usually was mentioned in the past. Although these caeca have no place in the generic definition, further information as to conformation and segment of origin will be of assistance in determining relationships of species. For other parts of the digestive system, esophageal valve, calciferous region of the esophagus, typhlosoles, etc., considerable information, derived from thousands of specimens, now is available. For those species that have been studied, all of the evidence from normal specimens is so invariable as to warrant the extrapolation indicated in the tentative generic definition below. Whether the slight variation in segment of intestinal origin that has been recorded is real or fictitious remains to be determined.

Much less information usually was provided about the circulatory system. No mention whatever of any blood vessel is to be found in one species description after another in various older contributions. Location of the last pair of hearts is the only character included in many other descriptions. The omissions never have been rectified for many species. The vascular system of *P. posthuma* was believed by Bahl (1921) to be characteristic of the genus but that assumption soon was shown to be incorrect as regards the hearts. Otherwise, and except for a gap in the ventral trunk of one species (see *P. elongata* below), uniformity has been found in the mass of material examined since 1923. In absence of any indications to the contrary, the vascular system now is characterized as in the tentative definition below.

Momentary observation of any live specimen enables one to note disappearance from sight and then reappearance, even of a major vessel, as it is emptied and refilled. Obviously, the volume of blood is insufficient to fill all vessels simultaneously. As a result, different portions of the system are empty after preservation and when empty may be unrecognizable or almost so in field preserved material. All or nearly all of the subneural trunk, for instance, often is not distinguishable. However, in a large enough batch, a specimen usually can be found in which blood is present in some part of the trunk, even in the preclitellar continuation. That anterior portion, as well as certain parts of other vessels, appears to have been unrecognized in the presumably better preparations, specially preserved in the laboratory, of the few earthworm species that were studied by morphologists. Their descriptions sometimes need to be supplemented or corrected from data provided in recent taxonomic contributions.

Our knowledge of excretory systems in *Pheretima* comprises results of Bahl's study of *P. posthuma* and several other unnamed but indubitably peregrine species. Conditions found in *posthuma* (Bahl, 1919) were assumed, as usual, to prevail throughout the genus. That may seem rather gratuitous as the genus supposedly comprises some 400 odd species. Material available to the taxonomist rarely is well enough preserved to warrant expenditure of the time and effort required to obtain the desired information. Specimens often are encountered in which structure is almost unrecognizable in the supposed micronephridia. The peritoneum occasionally has disintegrated so as to leave attached to the musculature scattered shreds superficially resembling micronephridia. Divergence from the *posthuma* norm presumably should be anticipated, if anywhere, in the supposedly primitive species for which Michaelsen erected the subgenus *Archipheretima*. However, no contra-indications to Bahl's assumption were recorded by any of those who have studied species of *Pheretima* during the last thirty years. If the excretory system is uniform throughout all species, the genus will have to be defined much as below.

All organs of the reproductive system, except ovaries, oviducts and clitellum, are now known to have disappeared in parthenogenetic morphs of various species. If *Pheretima* is to be defined, as *Eutyphoeus* was (Gates, 1959), without exceptions or the qualifications of the classical system, any mention of genitalia becomes impossible. Such few characters as now appear to be uniform in species with sexual reproduction are segregated in a separate paragraph. The large gaps in our knowledge of three very important somatic systems require that the definition be labelled tentative. Such designation will obviate, it is hoped, unnecessary erection of any genus merely because of some more or less unimportant anatomical difference.

All pheretimas collected in Burma west of the Irrawaddy-Sittang axis, with the exception of one series of a single species, probably have been listed in previous contributions. Many of the specimens secured after 1931 in the region east of the Irrawaddy-Sittang axis were not considered in the contributions of that period. Characterization of those worms became impossible when the author's records as well as the specimens, were destroyed in World War II. The loss is especially regrettable as the species are endemic, with interesting parthenogenetic polymorphism or geographical variation.

Tentative definition. Digestive system, without supra-intestinal and calciferous glands (calciferous tissues in low ridges that are not lamelliform in region of xiii?) but with a gizzard that develops in viii. Vascular system, with unpaired dorsal, ventral and supra-esophageal trunks, a subneural trunk adherent to the parietes, paired extra-esophageal trunks median to hearts, (latero?) esophageal hearts in some of segments x-xiii. Excretory system, meronephric — paired clusters of astomate nephridia in iv-vi with ducts opening into the pharynx — astomate, exonephric, very small, v-shaped parietal nephridia numerous in each segment back from iii — larger stomate nephridia with funnels in the same segment as body of tubule, on both sides of septa from xvi posteriorly, joining postseptal canals that pass to longitudinal, supra-intestinal excretory ducts opening at frequent intervals into gut. Setae, numerous, in a circle at equator of each segment from ii posteriorly. Ovaries fan-shaped and with several egg strings.

Male pores postclitellar. (Female pores intraclitellar?) Testes and male funnels enclosed in testis sacs. Seminal vesicles postseptal. Spermathecae diverticulate and pregonadal. Prostates, racemose, of mesoblastic origin, with ducts joined entally by the vasa deferentia.

Distribution. The Andaman Islands, the mainland of Asia from the Chindwin-Irrawaddy axis of Burma east through Yunnan and Szechuan provinces of China to include Korea and Japan, thence south to include New Guinea, Java and Sumatra. Whether any species are endemic in islands from the Marianas, Bismarck Archipelago, the Solomons and New Caledonia eastwards remains to be determined.

The generic range, as indicated above, comprises only areas where species are endemic. The peregrine forms have been carried almost everywhere by man and can be found today in greenhouses of North America, Great Britain and northern Europe, and in botanical gardens elsewhere in Europe. Nearly a score of species are now known to be domiciled outdoors in North America. Some of them also are present in Africa, South America, the West Indies, Australia, New Zealand, various oceanic islands such as St. Helena, Hawaii, etc. Hitherto there have been no records from Alaska, Greenland, the Sahara or Arabia.

PHERETIMA ANALECTA Gates, 1932

This species, as indicated below, may have arisen from an *andersoni*-like ancestor in which the GM series began at 18/19. Only the marking on 19/20 had been retained by most specimens from the range of subspecies *analecta*. Others (28 of 207 in 1932 collections) were variant, having a second marking of normal or reduced size at 20/21 or 18/19 (1 specimen) or a single normal marking at 20/21 (1 specimen). More interesting, however, were eight specimens on which the marking at 19/20 was halved so as to leave a small bit of unmodified epidermis at mV. In *P. a. rufula* on the Pegu Yomas across the Sittang valley from Toungoo, all markings have disappeared except the one on 18/19. That is now divided, each half circular to longitudinally elliptical and separated from the other by a space equal to 8-10 intersetal intervals. Further south on the Pegu Yomas, in subspecies *promota*, the genital marking at 18/19 has been retained without division but often is enlarged so as to reach beyond segmental equators of xviii and xix toward or even to 17/18 and 19/20. A similar origin may then be possible for the single large marking on the ten Thaton specimens of *andersoni* mentioned below.

PHERETIMA ANDERSONI Michaelsen, 1907

Genital markings of the two Amherst types on which this species was erected are anteroposteriorly short, rather spindle-shaped, centered exactly along six consecutive intersegmental furrows 19/20-24/25. Worms with similar markings (var. *typica*) were obtained in later years only at the type locality and at Chaungson. The markings, though usually six, were along 5-8 consecutive furrows of 18/19-26/27. Most of the worms hitherto referred to *andersoni* had fewer markings, of the same orientation (transverse to long axis of the body), but anteroposteriorly longer. Locations, again indicated by reference to intersegmental furrows though equators of two contiguous segments nearly were reached, one, two or three of 19/20-22/23, always on consecutive furrows when two or three markings were present. Distribution of these variant forms within a range comprising Mergui, Tavoy, Amherst and Thaton districts apparently was such as to contra-indicate further varietal names. A single genital marking present on each of ten specimens from Thaton (at northern end of the range) was so large that it could have originated from union of two or three markings at 19/20-21/22 or 20/21-21/22 (but cf. *analecta* above). Spermathecal pores on one of the ten specimens were just behind rather than at intersegmental furrows. The evolutionary trend seemingly indicated by available records is reduction in number of markings associated with more or less enlargement of all that were retained.

An unidentified worm from the Kyaukmedaung region of Tavoy district, where *andersoni* had not been recognized, was distinguished from that species as follows: Size (110 by 5 mm.), somewhat smaller. Color, red instead of blue though pigment probably is the same. Spermatheeal pores just behind intersegmental furrows. Genital markings, transversely elliptical, two pairs between equators of xix-xx and xx-xxi. Subsequent collections from the same area probably provided no further specimens (nor of typical *andersoni* for that matter). The worm is now regarded as a mutant in which the markings on 19/20 and 20/21 had been divided without loss of axial orientation. Supporting evidence for such a development is provided by a Mergui specimen in which the single marking on 20/21 was quite definitely dumb-bell shaped (also cf. subspecies *analecta* above).

The two types of *nemoralis*, collected in 1931, are of about the same size as *andersoni* but were distinguished by the red color and the presence of a pair of longitudinally elliptical markings centered at 20/21. None of the later collections from the Heimza Basin area contained similar specimens though more typical *andersoni* from the area had markings on 20/21 and 21/22. Types of *nemoralis* are now thought to be mutants of *andersoni* in which a single marking at 20/21 had been divided with loss of original axial orientation.

P. analecta, in the Salween district just north of Thaton and into the Karen Hills of Toungoo district now appears to have evolved from an *andersoni*-like ancestor presumably with a GM series beginning at 18/19. Differences from *andersoni* are few and if it were not for the size (50-124 by 3-5 mm. and 92-102 segments) which appears to be too small to allow copulation with any known individuals of *andersoni* (204-260 by 10-11 mm. and 120-134 segments) subspecies status would have been justified. Many specimens of *analecta* were heavily infested by several sorts of nematodes and gregarines but the parasites are unlikely to have brought about so much reduction in size.

P. velata Gates, 1930, present in Toungoo Karen Hills along with *analecta* but extending west into Karenni rather than Salween district, is of *andersoni* size or occasionally somewhat larger. Some heavily parasitized individuals were smaller than usual but were larger than all of the examples of subspecies *analecta*. Ecological requirements probably are similar to those of *andersoni*. The most efficient collector digging under the author's supervision obtained only one specimen at the type locality but in early morning, a month later, any number desired could have been gathered at the surface. Differences from *andersoni* are slight: Transverse banding of pigment in many specimens. Location of spermathecal pores (as rarely in *andersoni*) just behind intersegmental furrows. Enclosure of spermathecal diverticulum in a tough sac. Restriction of genital markings (an unpaired median or one pair) to region between equators of xvi and xviii. Interbreeding with *andersoni*, at least in Burma, is not contraindicated by size but is by the distributional discontinuity.

P. compta Gates, 1932, coexisting with *velata* in Burma but extending into Phre province of Siam, may have ecological requirements like those of *velata* and *andersoni*. Burmese specimens were immature (all secured in September, the usual breeding period in the plains) and were heavily infested with various sorts of parasites. Siamese adults were collected in November, perhaps at the surface after completion of cocoon deposition. Differences from *andersoni* appear to be of little importance except as to the genital markings which are always in three ranks at 18/19-25/26. No evidence for a tripartite subdivision of *andersoni* markings was found.

P. longicauliculata Gates, 1931, north of the *velata* and *compta* ranges and extending from Karenni (possibly also Kalaw and Taungyi), Kengtung and an adjacent portion of Yunnan to the Khun Tan mountains and Doi Sutep in Siam, is somewhat smaller (140-240 by 7-10 mm.) than *andersoni*. Differences again are slight except as regards the genital markings. These always are paired and transversely elliptical, at some or all of furrows 17/18-29/30. The markings are about the same as on the above-mentioned Kyaukmedaung specimen of *andersoni*.

P. labosa Gates, 1932, from the region of the Sino-Burman border north of Kengtung, like *andersoni* has unpaired genital markings, usually only one. This may represent union of two belonging at 21/22 and 22/23. All specimens, even those secured in October, were immature. Differences from *andersoni,* absence of pigment, smaller size of organs and of body, are slight.

P. sonella Gates, 1936, again from the region of the Sino-Burman border but to the west and near Namkham, has a single genital marking between equators of xxii and xxiv that could have arisen by union of *andersoni* type markings belonging at 22/23 and 23/24. A similar union of two or three markings was suggested above for certain Thaton specimens of *andersoni.* The six northern specimens, in part abnormal, were preserved in alcohol that had bleached any pigment that may have been present.

P. choprai Stephenson, 1929, across the Irrawaddy River and to the northwest in Myitkyina district, is known only from two types also alcoholic. Pigment of the *andersoni* sort may have been present. Genital markings are circular or nearly so, at 21/22-26/27 (at 17/18 once) and like those of *andersoni* except that the marking at 21/22 is completely separated into two portions. Other differences from *andersoni* are: male porophores much larger; spermathecal pores apparently slightly larger though soma size is smaller and located just behind intersegmental furrows; a slight tumescence present in front of each spermathecal pore.

Genital markings of the above-mentioned forms are not slight epidermal modifications of the sort present in various other genera but are distinctly delimited. Furthermore, each is invariably associated with a mass of glandular tissues in vertical cords that usually (always?) is surrounded by a strong sheath. Markings invariably are present and just as invariably are restricted to a region comprising segments xvii-xxx. All of these species are closely related and could have evolved from a form very much like *andersoni.* That ancestral form, though by no means primitive, may have arrived in Burma before other pheretimas as the *andersoni* group and *feai* alone have gotten across the Irrawaddy-Sittang axis without assistance from man. Because of the invariability of presence or absence of genital markings in ranges that extend down nearly through the north-south limits of Burma, *andersoni* and *feai* are believed to be specifically distinct though there are no size differences to contra-indicate breeding. Except in the far north where the Salween and Irrawaddy Rivers were crossed, *feai* just gets into Burma in hills at the Siamese border. In Burma the two ranges must about meet at Kawkareik. Overlapping of ranges in Siam is to be expected. Solutions to many of the problems posed by Burmese earthworms must be sought in the adjacent east. Unfortunately, little is known about the oligochaetes of those lands.

PHERETIMA ANOMALA Michaelsen, 1907

Abnormality. Clitellum reaches 17/18 on the right side. Segments xix-xxiii are involved in a helicometamere that terminates ventrally at each end. Three prostates are present on the right side, with pores on xix, xx, and xxi, the male deferent ducts of that side joining the duct of the anterior gland. Segments in which intestinal caeca arose, unfortunately, were not determinable.

PHERETIMA BIPORA (Beddard, 1901)

Seminal vesicles that were supposed to be present in segment x of the types undoubtedly are nothing more than dorsal portions of testis sacs, if not mere masses of coelomic coagulum. Hearts probably are present in xiii. Though types are extant they are of little if any value. *P. gemella* Gates, 1933 (types and all other specimens destroyed during the war) and *floccllana* Gates, 1949 (named in a manuscript submitted in 1941) probably differ from each other and from *bipora* mainly with respect to characters such as these: shape and location of preclitellar genital markings; sizes of pseudocopulatory chambers, penes and pseudopenes; shape of prostatic ducts. *P. gemella* and *floccllana* are now placed in the synonymy of *bipora*. Whether any of the differences mentioned above, or whether other characters such as number of pseudocopulatory chambers are correlated with distribution so as to permit recognition of geographical races, cannot be determined until lost collections are replaced. The number of pseudocopulatory chambers now appears to be larger in a southern portion of the Mergui district (Burma) that may be near the middle of the species range. Parthenogenesis is suspected in some portions at least of the range, though supporting evidence cannot now be presented.

Relationships probably are closest to *P. anomala* but neither species can be derived directly from the other.

Coelomic copulatory chambers are uncommon in species with manicate intestinal caeca. They have been recorded only from the Chinese *pacta* Gates, 1935, which has stalked glands opening to the exterior through small tubercles (like those of *diffringens*, *hawayana*, etc.) and the peregrine *schmardae* (of unknown origin). Each of those species has retained the primitive spermathecal battery with pores at 7/8-8/9. Derivation from a quadrithecal form involves addition of a single pair of spermathecae in vii and then of another pair in v, associated at some time or other with loss of the pair belonging in ix. Early stages in evolution of copulatory chambers are shown by several species but for each of them there are geographical or anatomical contra-indications to close relationships with *birmanica.* If copulatory chambers evolve as rapidly as indicated by *papilio,* relationships of *birmanica* to species with superficial male pores ought to be considered. One species, the Burmese *defecta,* has a spermathecal battery like that of *birmanica.* To derive the latter from a form like *defecta,* but with spermathecal pores still on intersegmental furrows, only the following changes would be required: demarcation of a small circular area of epidermal modification around each spermathecal pore and withdrawal of the porophore into a shallow invagination with transversely slit-like lumen; invagination of the male porophore into the coelom and elongation of the smaller circular area containing the pore into a conical penial body.

PHERETIMA BIRMANICA (Rosa, 1888)

The typhlosole, in Dehra Dun specimens, begins in the caecal segment and in the next 11-15 metameres is low, opaque, yellowish, slightly thicker dorsally and hence triangular in cross section, with low vertical ridges on the lateral faces. Then for several segments the typhlosole occasionally seems to be completely lacking. Thence, to its end, the typhlosole is translucent and of rather nondescript shape.

Seminal vesicles of adults are small and appear to be juvenile. Information as to maturation and exchange of sperm no longer is available. Reproductive organ polymorphism has not been found (400+ specimens examined). Male sterility is suspected.

PHERETIMA DEFECTA Gates, 1930

This species was erected on an athecal posterior amputee with manicate intestinal caeca. Seminal vesicles were quite juvenile or rudimentary. Prostates were lacking but ducts and male porophores were present. Reproduction presumably would be parthenogenetic. The type belonged to an intermediate morph, of the fourth order if spermathecae and prostates had been eliminated concurrently, or of a fifth order if spermathecae had been lost before the prostates. Male porophores were like those of *jacita* in some of eight subsequently secured individuals one of which had a diverticulate spermatheca of the sort present in *jacita*. Testis sacs were lacking in one of the specimens, a condition that has been found in several parthenogenetic morphs evolved in other species of *Pheretima*. *Pheretima jacita* Gates, 1931, the only other taxon with manicate intestinal caeca in the *defecta* area, has small but normally developed spermathecae, large seminal vesicles and prostates. Reproduction is assumed to be sexual and biparental as sperm are matured and exchanged in copulation. *P. jacita* then is of or very like the H morph from which the parthenogenetic intermediate morphs have evolved. *P. jacita* is suppressed as a synonym of *defecta*. If relationships are with Burmese species gross changes in the genitalia have been involved, in the spermathecal battery if with *manicata* and *canaliculata* Gates, 1932, in the male terminalia if with *birmanica* (*q. v.*).

PHERETIMA ELONGATA (Perrier, 1872)

India

Karachi, Sind, September, 0-3-0. K. N. Bahl. (Four specimens, unlabelled, may have been from the same locality.)

Poona, Bombay Presidency, garden of Ferguson College, 0-0-10. K. N. Bahl.

Kurnool, Madras Presidency, from black earth, September, 143-99-516. W. D. Sutton.

External characteristics. Some of the clitellate Kurnool worms are small for this species, 90-100 by 4 mm. Genital markings of Rewa specimens, in xix-xxiii (56 specimens), xix-xxiv (2). Spermathecal pores, minute and superficial, at 5/6-6/7, whenever present.

Internal anatomy. Pigment unrecognizable in special longitudinal muscle band at mD.

Dorsal blood vessel often apparently continued forward to a bifurcation just in front of brain, the two branches very shortly disappearing. However, within the tissues associated with the pharyngeal bulb, the real dorsal trunk — larger than the median branch just mentioned — passes forward to the brain underneath which it bifurcates, the branches reuniting above the subpharyngeal ganglion to form the ventral trunk. The latter is continued posteriorly into vii where it usually turns to run upwards on the anterior face of septum 7/8, either on the right or on the left side. Occasionally the trunk bifurcates, both branches passing up on anterior face of 7/8, one branch always much larger than the other. The ventral trunk, in the smallest juvenile that has been dissected, at first appears to bifurcate in front of 7/8 but a slender, colorless (functionless?) filament continues on through the septum to a bifurcation at equator of viii. There each bifurcation very shortly widens (thence onwards filled with blood) and then branches several times, one of two larger branches joining the extra-esophageal trunk, the other opening into a ventral portion of the heart of ix below the white bulb. The posterior portion of the ventral trunk ends exactly, in every specimen, with the hearts of ix. Between circumpharyngeal connectives which are assumed to be segmental commissures of i and septum 4/5 two pairs of vessels open into the ventral trunk, one shortly behind the connectives, the other on the anterior face of 4/5. These paired vessels appear to be ventral remnants of segmental commissures of ii and iv, the large gap between indicating site of former junction of commissures of iii. A pair of thin red lines, just recognizable in that gap in the smallest juveniles that were examined, may be still unaborted portions of the usually missing commissures. Segmental commissures of v, on one or both sides, may still join ventral trunk in adults. Commissures of vi-vii, large dorsally, seem to have lost their connections with the ventral trunk. No vessels from dorsal trunk to gizzard were recognized and no trace of commissures of viii was found. The pair of commissures behind the gizzard, formerly thought to belong to segment viii (Gates, 1926, p. 450), is now attributed to ix. Commissures of x-xii always open into ventral trunk and dorsally into the supra-esophageal. Until dorsal bifurcations to dorsal trunk have been recognized and found to be functional, hearts of x-xii must be characterized as esophageal. Hearts of xiii are present and normal, incomplete ventrally or lacking. Incomplete rudiments, always dorsal, comprise a short stem or stalk from the supra-esophageal trunk of about the same thickness as a normal heart and a terminal spheroidal or pear-shaped portion that is much thicker and large enough to be in contact with both septa 12/13 and 13/14. The stem, from the supra-esophageal trunk is red or white but the terminal portion always is dark and filled with blood. No slightest trace of a ventral continuation was found even at the ventral trunk. The variation in hearts of xiii in a Rewa series of 58 normally polythecal worms is shown in Table 3. Subneural trunk, adherent to parietes, often appears to pass out from under the nerve cord to right or left side shortly behind xiii. Actually, however, a slender and apparently functional continuation of the trunk often is recognizable for some distance in front of xiii, occasionally almost to anterior end of body. A branch passing off behind the seeming lateral bend of the subneural is called smaller though occasionally nearly as thick. Larger and smaller branches, in a specimen with no hearts in xiii, join an extra-esophageal trunk, but in 55 worms turn dorsally in xiii and open into the supra-esophageal trunk. Large and small branches, in specimens with hearts in xiii, join supra-esophageal in xii. Extra-esophageal trunks turn laterally and pass off from gut in xiii or xiv.

Typhlosole, simply lamelliform, beginning abruptly in region of xv-xviii (10 specimens), gradually becoming lower posteriorly, hinder half translucent, ending abruptly in 116th (of 187), 133rd (of 213), 137th (of 224) segments, in cxxviii (of a worm that had lost its tail well behind that segment), in lxx (worm with a six-segment tail regenerate at 98/99).

Spermathecal batteries, when present in Poona and Satna worms, are small 1-1 and 1-2, 1-1 and 2-2, 1-3 and 1-2, 1-4 and 1-1, or defective (1-0 and 1-1), Poona, all defective in Satna worms, 2-0 and 4-0, 0-2 and 0-4, 0-3 and 0-3, 0-2 and 0-0. A normally polythecal battery, a condition not hitherto reported from Indian material, characterizes each Karachi and many Rewa worms. Variation in numbers is shown in the table below. Spermathecae are lacking in most of the Kurnool worms. Thecal individuals from that locality have only one or two spermathecae at each of one, two or three of the normal four locations.

Reproduction. Data for sperm maturation and exchange in copulation no longer are available. Parthenogenesis and male sterility is anticipated in atheeal individuals as well as in many of the worms with defective batteries.

Castings. Observations on casting deposition were made in a patch of sticky black earth, well shaded by a large tree, where *elongata* was the only species present. Tower-shaped castings never were found. Intestinal ejecta occasionally was in a single uninterrupted cord 2 mm. thick and 20-40 mm. long. More often cords were deposited in irregular piles 10-20 mm. high and 20-35 mm. wide.

Remarks. The vascular system of *elongata,* in an anterior portion of the body, is more divergent from the supposed generic norm than in any other species for which information now is available. Whether the deviations arose before or after appearance of parthenogenesis is unknown. Some of the little available evidence (as yet unpublished) that is provided by sexual morphs from the probable homeland of the species hints at a possibility that hearts may have been added in xiii after reproduction had become asexual. This might then mean that somatic as well as genital evolution can proceed more rapidly in asexual than in sexual forms.

P. stelleri (Michaelsen, 1891) and some of its inadequately characterized subspecies or varieties may have to go into the synonymy of *elongata.*

P. elongata has been widely distributed throughout the world, presumably by man. Successful colonization appears to have been limited to tropical lowlands. The original home of the species probably is to be found in islands to the southeast of the Asiatic mainland.

TABLE 3

Hearts of xiii in a Rewa series of *Pheretima elongata*

Both hearts present, complete and normal		34 specimens
One heart normal, one rudimentary		8
Right heart normal	7	
Left heart normal	1	
One normal heart present		5
On right side	2	
On left side	3	
Both hearts rudimentary		3
One rudimentary heart present		4
On right side	2	
On left side	2	
No hearts or rudiments		4
Total		58

TABLE 4

Variation in number of spermathecae in *Pheretima elongata* from Karachi and Rewa

Segment v	Segment vi	Specimens	Segment v	Segment vi	Specimens
2-2	1-3	1	3-3	2-4	1
2-2	2-3	2	3-3	3-2	1
2-2	2-4	1	3-3	3-3	13
2-2	3-3	3	3-3	3-4	2
2-3	2-2	1	3-3	3-5	1
2-3	2-3	1	3-3	4-2	1
2-3	2-4	2	3-3	4-3	1
2-3	3-2	3	3-3	4-4	2
2-3	3-3	6	3-3	5-4	1
2-3	3-4	3	3-4	3-4	2
2-3	4-3	3	3-4	4-2	1
3-2	2-2	1	3-4	4-3	1
3-2	2-3	3	3-4	4-4	1
3-2	3-3	2	4-2	3-4	1
3-2	3-4	1	4-3	3-3	2
3-3	2-3	3	4-4	4-3	1

"2-2" means two spermathecae on the left side, two on the right side, in segment v or vi according to the column.

PHERETIMA EXIGUA Gates, 1930

Seminal vesicles of adults are small and those of xi are included in the testis sac. Information as to maturation and exchange of sperm no longer is available. Prostates frequently are small, rudimentary or lacking. Individuals so characterized are of second order intermediate morphs evolving toward an anarsenosomphic stage (R morphs). Other morphs were unrepresented in collections comprising about 600 specimens.

Evolution towards an R morph is sufficiently advanced to warrant confident anticipation of parthenogenesis.

P. exigua does not appear to be closely related to any of the Burmese endemics. Anatomically, the species is nearest to *diffringens*, which may have come originally from some part of China or Japan.

PHERETIMA FACETA Gates, 1932

North Andaman, Andaman Islands, on the moist jungle path between Port Bonington and Base Camp, 24.xii.33, 0-0-1. H. S. Rao. (Indian Mus.)

External characteristics. Size, *ca.* 100 by 4 mm. Segments, 114. Pigmentation unrecognizable (alcoholic preservation). Prostomium epilobous, tongue open. Setae: 26/iii, 38g/viii, 48/xii, 53/xx, viii/16, xviii/10, xvii/14, xix/16. First dorsal pore, at 12/13.

Spermathecal pores minute (not slit-like), only slightly behind intersegmental furrows. Female pores possibly represented by two minute, grey spots close together on roof of a transversely slit-like depression. Male pores slit-like and of about the same size as the female pore depression, each at center of a small, transversely elliptical area surrounded by several concentric furrows. The furrowed area is slightly protuberant.

Internal anatomy. Septum 9/10 represented by a thin membrane inserted on gut behind heart of ix and attached peripherally to 10/11. Intestinal caeca simple, arising in xxvii and extending into xxiii. Typhlosole, which begins in caeca segment, simply lamelliform and at first not quite one mm. high. Only heart of ix (lateral) on left side, both hearts of x apparently esophageal, hearts of xi-xiii latero-esophageal. Lymph glands present behind prostatic segments.

Testis sacs unpaired, ventral, between nerve cord and ventral blood vessel. Spermathecal diverticulum passes into duct at parietes, the stalk portion sinuous or in very short zigzag loops.

Reproduction. Spermatozoal iridescence is obvious on male funnels and in ental portions of spermathecal diverticula. As sperm had been matured and exchanged in copulation, reproduction is assumed to be sexual and biparental.

Remarks. Markings like setae in follicle apertures are lacking or unrecognizable on i of this worm. Setae have however been found in the peristomium of head regenerates in species of *Perionyx*. Presence of setae in i also has been recorded for a Chinese species of *Pheretima*.

Location of spermathecal pores, in this specimen, is not as distinctive as in the types.

Ten specimens from Ponape, Natsushima, Truk Islands, in the Pacific have been referred to *faceta*. Some, if not all, were abnormal and parthenogenesis is suspected (spermathecae of viii often had no diverticula). The misidentified worms appear to be more like *P. javanica* (Kinberg, 1867) than *faceta*.

Protuberances on xviii warrant a suspicion that male porophores may be retractile into slight parietal invaginations.

PHERETIMA FEAI (Rosa, 1888)

These worms were not obtainable by digging over upper layers of soil but in early morning hours, at some time during October-November, vast multitudes crawl around on the surface until killed by heat or sunlight. They are so snake-like in appearance that coolies refuse to gather them, even for a considerable addition to the usual wage.

The worms are distinguishable at present from *andersoni* only by absence of genital markings and a slight but definite difference in color. They were suspected for some time of being merely a mutant population of *andersoni* restricted to a small area around the town of Kawkareik in the hills of Amherst district near the Siamese border. That was subsequently contra-indicated by individuals found on Mt. Kambaiti, far to the north and west of the Salween River, in an area where *andersoni* is unknown. Transportation from one locality to the other seems highly improbable. For the present, ornate taxa (i.e., with genital markings) are allowed to retain species status independent of *feai*. Nevertheless, absence of externally recognizable indications of geographical variation in so large a range (even if the two sites are at or near southern boundaries) now seems unusual.

Tropical soils are commonly thought to be poor in organic matter. Yet down below the layers usually dug over by collectors earthworms do find an adequate supply of food. So much, indeed, that all species living at those depths are of medium to large size; diameter when strongly contracted 6-15 mm.; length, when contracted, to 600+ mm.

PHERETIMA GLABRA Gates, 1932

This species, *tenellula* Gates, 1932, and *victa* Gates, 1936, respectively, are known only from the description of 24, 49 and 16 types. All specimens of *glabra* and of *tenellula* had large seminal vesicles and prostates but were athecal. As externally adhesive spermatophores are unknown in the genus, reproduction presumably is uniparental even though sperm are matured (cf. R morph of *P. anomala*). Each specimen of *victa* had one pair of spermathecae but seminal vesicles were small (juvenile or rudimentary), those of xi within dorsal extensions of the posterior testis sac. The spermathecal diverticulum probably was abnormally elongated (at least relative to length of main axis) and without definite differentiation into stalk and seminal chamber. The main axis, though shorter than the diverticulum, may have been normally proportioned. Spermatozoa certainly were lacking in the spermathecae and testes probably were sterile. Seminal grooves are rare in the genus *Pheretima*. Those of the three taxa, like the genital markings or porophores on which they are located, differ mainly in amount of anterior extension from site of the male pore. *P. tenellula* and *victa* are placed in the synonymy of *glabra*. Estimation of relationships is difficult as no evidence has been recognized that would indicate whether types of *victa* are of an H_p morph or of some intermediate morph that already had lost one or more pairs of spermathecae.

PHERETIMA HOULLETI (Perrier, 1872)

India

Andaman Islands, September 1932-May 1933, 0-0-1. H. S. Rao. (Indian Mus.)

Bombay, August, 1958, 0-0-2. V. B. Tembe.

Philippine Islands

Sampaloc, Manila, September 1958, 1-11-9. Magdalina Cantoria per Y. Kondo.

External characteristics. Size (contracted), 75-85 by 2-4 mm. Segments (Philippines), 85, 89 (old posterior amputees), 98, 99 (3 specimens), 100 (3), 101 (3), 102; other specimens are recent posterior amputees. Pigment obviously present, the dorsum of two Manila worms appearing to be almost black. Prostomium epilobous, tongue open (20). First dorsal pore at 10/11 (20): whether a more or less pore-like marking at 9/10 (once at 8/9), sometimes indicated presence of a functional pore, was not determinable. Spermathecal pores about ½C apart. Female pore median (18).

Internal anatomy. Pigment, reddish brown, restricted to dorsum, on inner face of epidermis, through circular muscle layer, on outer face of longitudinal muscle layer, sometimes dense in special longitudinal muscle band at mD, lacking or very sparse immediately under intersegmental furrows and around setal follicles. Pigment is present between the follicles though an equatorial band containing the setae often appears externally to be unpigmented. The longitudinal muscle band at mD is distinct back from the first dorsal pore.

Intestinal origin in xv. Intestinal caeca, short, arise in xxvii and pass forward into xxiv or xxiii, dorsal and ventral margins more or less deeply constricted at septal insertions. Typhlosole, rudimentary in xv-xxvi, from caecal segment rather lamelliform but with low, vertical ridges laterally, ending abruptly in 63rd (of 99) or 65th (of 103) segments. Low segmental ridges running posterolaterally from the typhlosole do not end abruptly at level of hind end of typhlosole as they do in *posthuma*.

Dorsal blood vessel, complete, bifurcating under brain, branches passing ventrally and uniting over subpharyngeal ganglion to become the ventral trunk. Between that junction and septum 7/8 only five pairs of segmental branches from the ventral trunk have been recognizable, one of a pair sometimes apparently lacking. Only one of the segmental commissures of vi has been traceable to the ventral trunk in many of the worms. Segmental commissures of vii usually pass to the ventral trunk. Unaborted dorsal portions of commissures of viii pass to the gizzard, no remnants of ventral portions having been found. One heart of ix, on the right or the left side, obviously is lateral — directly connecting dorsal and ventral trunks. The other heart of ix which may be of the same size dorsally or much slenderer usually becomes almost filamentous (though sometimes still red) further down, the ventralmost portion joining the ventral trunk about opposite the unmodified heart of ix. Hearts of x-xiii appear to be latero-esophageal though blood usually is lacking in each of the dorsal bifurcations. Extra-esophageal trunks, median to segmental commissures, pass onto ventral face of gut in region of ix and thence posteriorly are close together but not in contact. The trunks often appear to turn off from the gut in xiii and to pass to the parietes on which they pass back to region of intestinal caeca as if posterior lateroparietal trunks. No evidence has been found, even in best preservation, of extension behind caecal segments. Subneural trunk, adherent to parietes, probably always complete but when empty in preclitellar segments almost or quite unrecognizable. Blood glands present in v-vi. Lymph glands, present behind xv, show considerable regional and individual variation in size. When large they are horizontally U-shaped.

Testes discoidal to nearly spheroidal. Little or no coagulum in testis sacs. Male funnels small but plicate. Male gonoducts, straight or slightly sinuous just behind funnel septa (without epididymis), come into contact near 12/13 and appear to unite, the common duct passing into prostatic duct slightly below the ental end. Seminal vesicles, small, though rather soft of juvenile shape. Pseudovesicles, when present, quite rudimentary and in xiii-xiv. Prostates, large, well developed, xvi, xvii-xx, xxi, xxii, xxiii. Ducts, muscular, in a C- or U-shaped loop. Copulatory chambers with anterior and posterior glands.

Spermathecae, each with the usual stalked gland. Ampullae collapsed, empty or with but little coagulum ectally. Seminal chambers of diverticula translucent. Ovaries fan-shaped, with several to numerous short egg-strings.

Reproduction. Spermatozoal iridescence is lacking on male funnels and in spermathecae of all specimens as well as in a number of others (not listed above) that have been examined in recent years. Spermathecal ampullae of other specimens with clitellum at maximal tumescence may be distended by a coagulum that is translucent entally and opaque ectally but again without spermatozoal iridescence. Such worms probably are male sterile. If so, reproduction must be parthenogenetic, at least in many of the places to which *houlleti* has been transported. Determination of status and relationships of the taxon (cf. Gates, 1956, p. 222) awaits information as to anatomy of worms in the unknown original home presumably somewhere in southeast Asia. Male sterility, according to data now available from recently colonized areas, may have appeared shortly after acquisition of ability to reproduce parthenogenetically but before drastic modification of genitalia had gotten under way. Accordingly, further studies of variation in *houlleti* can be expected to provide clues as to the nature of the steps by which those modifications are brought about.

Castings. Individuals of this species crowded in earth around plant roots in small pots, during July and August at Allahabad, deposited much of the intestinal ejecta on the surface of the earth. Castings were irregular cords, isolated or in low piles. Tower-like castings were not found. Rangoon worms, kept in much larger pots where they were less crowded, did not cast on the surface. Deposition under ground probably is usual. Castings contained no macroscopically recognizable plant materials. The worms obviously are geophagous.

P. houlleti is one of the three species that Darwin seems to have held responsible for production of tower-like castings "in extraordinary numbers" at Nice. Towers also are not deposited by the other two, *Perichaeta luzonica* (now *Lampito mauritii*) and *Perichaeta affinis* (now *Pheretima posthuma*). Tower-castings from Calcutta, supposedly erected by some species of *Perichaeta,* probably were produced by a species of *Eutyphoeus*, possibly *E. waltoni* (Michaelsen, 1907). Individuals of that and several other species of the genus have made tower-like castings under controlled conditions in the laboratory.

Remarks. A size of 100-135 by 5 mm. had been reached by some Jubbulpore specimens (already listed elsewhere) that probably were obtained at a site unusually rich in some sort of organic matter.

Tail pieces of 28-35 segments in the Manila lot probably had been autotomized. Similar tail portions of two worms as preserved had not yet been completely separated off. Autotomy, as in *P. agrestis* (Goto & Hatai, 1899), probably is easily induced and quickly accomplished. Live specimens should be picked up by the anterior end rather than posteriorly.

One copulatory chamber of each Bombay worm had a single GM gland on its posterior face. Other deviations from the characteristic *houlleti* norm, such as larger size of the Jubbulpore worms or presence of a second stalked gland on an occasional spermathecae, are not unknown. Penial bodies, when any question as to identification has arisen because of such deviations, always have enabled reference of the worm to one of the three closely related forms, *houlleti, campanulata* and *meridiana.* Dissecting out the penial body has not been attempted by most of those who have studied any of these forms but is not especially difficult. Recognition of typical characteristics of the penial body in microtome sections is likely to be far from easy.

Relationships of the *houlleti* group are with *P. virgo* (cf. below).

PHERETIMA ILLOTA Gates, 1932

This taxon is known only from the description of two athecal specimens, secured across the border in China. Seminal vesicles were small, if not rudimentary, probably juvenile. An A morph now warrants confident anticipation of parthenogenetic reproduction. As seminal vesicles are small, male sterility is suspected.

An A morph such as this provides few and but slight clues for determination of relationships. If male porophores are the same as in the ancestral H morph they might be of some assistance. Although the only modifications of the porophores hitherto recognized in genital polymorphism are regressive, positive changes perhaps ought to be looked for as they have appeared during evolution of subspecies, i.e., in geographical polymorphism.

More intensive collection in the proper areas can be expected to turn up the intermediate morphs that will provide proof of relationships. Somewhat less confidently perhaps a sexual H morph can be anticipated (cf. *rimosa*).

PHERETIMA MALACA Gates, 1936

This species is known only from the description of 18 specimens obtained at two widely separated trans-Sittang localities. Spermathecae may have been normal in two of the types but in others were abnormal (3 specimens) or rudimentary (3). Seminal vesicles were juvenile or rudimentary, the anterior pair included in a testis sac. Prostates were small, confined to xviii. Testis sacs were paired or unpaired and then U-shaped or annular. No evidence of maturation or of copulatory exchange of sperm was found, though 17 specimens had a fully developed clitellum. Male sterility, and consequently parthenogenesis, is anticipated. *P. malaca* is much like *papulosa* (Rosa, 1896) which also has small seminal vesicles, the anterior pair enclosed in a testis sac. The major morphological difference between the two taxa is absence in *malaca* of the spermathecae that open at 5/6 and 7/8 in *papulosa*. Such a difference was long recognized as sufficient justification for specific distinction. However, it is now known that the first and last pairs of spermathecae in a sexthecal battery have disappeared from certain intermediate morphs evolved, in at least three species of *Pheretima*, since establishment of parthenogenesis. Until much more is learned about somatic as well as genital variation in *papulosa* in its still unknown original home, relationships with *malaca* may have to remain uncertain.

PHERETIMA MANICATA Gates, 1931

All specimens of this species secured from the lowlands of Amherst and Thaton districts (the earthworm fauna in the hills of those districts is almost unknown) have had small male porophores, and also on xviii two longitudinal genital markings reaching or even crossing 17/18 and 18/19. As that combination of characters appears to be geographically restricted, var. *typica* is now considered to be a subspecies. In worms from the Toungoo Karen Hills north into Yunnan and west into Thailand, size of male porophores is variable and genital markings though not longitudinal are of various shapes and locations. These northern worms from higher elevations are easily distinguishable externally. They were previously known as var. *decorosa* which is now given status of a subspecies. The area in which *P. m. decorosa* was found is much larger than that of *P. m. manicata.* Quite possibly material destroyed during the war would have permitted recognition of more than one local race in the northern portion of the species range.

Anatomically, *P. manicata* is close to but one Burmese species, *arboricola* Gates, 1936. The latter is chiefly distinguished, aside from several minor characters, by presence of a sort of "creeping sole" in the ventrum. This development, in acaecal arboricolous forms was thought by Michaelsen to justify recognition of a subgenus *Planapheretima.* In *arboricola* the sole is associated with highly specialized manicate intestinal caeca. *P. vallata* Chen, 1946, from Szechuan Province (China) is distinguishable from *manicata* only by the spermathecal diverticula which are like those of *diffringens.*

PHERETIMA OSMATONI Michaelsen, 1907

North Andaman, Andaman Islands, on the moist jungle path between Port Bonington and Base Camp, 24.xii.33, 0-0-1. H. S. Rao. (Indian Mus.)

External characteristics. Size, *ca.* 185 by 8 mm. Segments, *ca.* 126 (posterior amputee?). Pigment probably is present, at least in dorsum of preclitellar segments, each seta in a small, longitudinal, unpigmented stripe that does not reach either intersegmental furrow. Prostomium epilobous, tongue open. Setae: vii/8, viii/10, xviii/10, (present ventrally on xvi?).

Spermathecal pores, minute, superficial, each at center of a small, smooth area of shortly elliptical outline, porophore possibly slightly retractile into parietes so as to produce appearance of a slit-like external aperture. Female pores unrecognizable.

Internal anatomy. Pigment, probably dark red. Septum 9/10, as previously, represented only by a ventral rudiment. Intestinal caeca simple, reaching forward only into xxvi or xxv.

Typhlosole simply lamelliform, 1+mm. high shortly behind its origin in caecal segment. Hearts present on both sides of ix (lateral); hearts of x large and apparently esophageal; hearts of xi-xiii latero-esophageal. Lymph gland, in each postcaecal segment, continued into a long and laterally directed lobe on each side.

Testis sacs unpaired and ventral, ventral blood vessel above or resting on roof of sacs, nerve cord well below sacs. Penisetal follicles, coelomic, strongly muscular, lateromesially flattened, coming to a point dorsally and of triangular shape, one just lateral and one just median to duct of accessory glands, the median follicle somewhat smaller. Soft, white and presumably glandular material apparently passes into parietes between lateral penisetal follicle and prostatic duct but a stalk was not distinguishable. Common duct of the muscular-stalked glands T-shaped, the horizontal limb thick and fairly straight, the leg of the T slenderer and in the parietes even more narrowed. Pseudovesicles of xiv fairly large, one containing a brown body.

Spermathecal duct narrowed within the parietes. A glandular collar is unrecognizable. Diverticulum passes into spermathecal duct at the parietes.

Reproduction. Spermatozoal iridescence on male funnels and in seminal chambers of spermathecal diverticula is brilliant. Reproduction presumably is sexual and biparental.

Remarks. Pigmented areas are barely recognizable because of alcoholic browning.

Genital markings and associated glands appear to be lacking.

PHERETIMA PAPILIO Gates, 1930

A good series of this species was obtained at a site not far from the west bank of the Irrawaddy River in Prome district, somewhat south of the town of Prome. No village was nearby, though one had been there some years before. The worms were recognized by the collector, K. John, as belonging to *P. papilio* and he was able to mention the trans-Sittang localities at which he had secured specimens with similar spermathecal and male porophores. Transportation, presumably by man, must be responsible for the presence of that isolated colony well away from the region where it is endemic.

Specimens from the southern three of the four Tenasserim districts have been sufficiently uniform throughout that area to permit recognition of var. *typica* as a geographical subspecies, *P. p. papilio.* A satisfactory morphological characterization must, however, await re-assembly of lost data. A northern subspecies, *P. p. hiulca,* can be morphologically characterized more adequately, by reference to invaginations in the male porophores and possibly also to those associated with the spermathecae. An intermediate stage in evolution of the male porophores is indicated by the only records now available (Gates, 1932) for Thaton district. More variation than in the southern subspecies is probable in *P. p. insignis.* Male porophores of worms in one section of the Pegu Yomas (var. *fracta*) may be in a somewhat less advanced stage than in the Toungoo Karen Hills of the Shan Plateau.

Within the limits of an apparently good species, invaginations have evolved in association with the spermathecae. Superficial male pores have become deeply invaginate. All that is needed to provide the sort of copulatory chamber characteristic of many species (cf. *birmanica*) would seem to be very considerable narrowing of the opening into the invagination.

PHERETIMA PAUXILLULA Gates, 1936

This species is known only from the original description of 18 sextheeal worms with pores at 4/5-6/7. Seminal vesicles were small or very small (presumably juvenile or rudimentary), those of xi included within the testis sac. Sperm, in each spermatheca of the five dissected specimens, were lacking and testes probably were sterile. *P. digna* Chen, 1946, known only from the description of five types from Szechuan, is distinguishable only by the slightly greater length of the intestinal caeca and by the looping of the spermathecal diverticula. Absence of spermathecae opening at 4/5 "usually" is the only datum, except for inclusion of seminal vesicles in the posterior testis sacs, that would justify suspecting parthenogenesis. Certainly, variation in number of spermathecae is very much more common in parthenogenetic forms than in species with obligatory biparental reproduction.

PHERETIMA PLANATA Gates, 1926

Siliguri, Bengal, India, compound of the Dak Bungalow, 30/xi/35, 0-0-2. (Indian Mus.)

This is the second record of this Burmese species from India, the other being South Cachar in Assam.

PHERETIMA POSTHUMA (Vaillant, 1868)

India

Udaipur, Rajputana, August, 0-0-5. M. M. Goil. 0-4-9. Ella MacLeavy.
Rawalpindi, Punjab, May, 0-8-4. F. G. Dickason.
New Delhi, July, crawling about on a road in a private compound after heavy rain, 0-0-79.
Jalla, Patna, Bihar, March, 0-9-4. R. C. Lacey.
Cuttack, Orissa, February, 0-0-15. H. S. Chaudhry.
Bombay, August, 1958, 0-0-6. V. B. Tembe.

External characteristics. Segments (Bombay specimens), 113, 114, 115 (2 specimens), 116, 117. (Cf. Table 6.)

Genital markings in the specimens listed above are in the usual situations, in the setal circles of xvii and xix. Variation in segmental location but not from equatorial position does occur. Markings in a small lot recently received from the Philippines are located as follows: in xvii and xix (3 specimens), lacking on one side of xix (1), an extra pair on xvi (1), an extra pair on xx (1). Location of the markings in an Allahabad series is shown in Table 5.

Internal anatomy. Pigment, within the circular muscle layer, present sparsely in the ventrum though recognizable externally only in the dorsum, is brown. The special longitudinal muscle band at mD, in relaxed as well as contracted specimens, is present and distinctly outlined back from 12/13.

Esophagus in x-xiii (relaxed specimens) with slight circular and longitudinal furrows that mark off on inner wall fairly uniform squares to produce a pavement block appearance (no ridges or lamellae). Intestinal origin in xv (15 specimens). Intestinal caeca, arising in xxvii (15 specimens), usually short, reaching to 25/26, into xxv, or rarely just into xxiv, margins often smooth. Typhlosole, from caecal segment low and simply lamelliform, ending abruptly (Table 6) in region of 88th-91st segments. From each side of the typhlosole in each segment behind xxx an obvious but low ridge (contracted as well as relaxed individuals) passes off posterolaterally and through three segments to a low ridge on floor of gut at mV. Posteriorly the ridges do not get that far around but end abruptly at level of hind end of typhlosole.

Dorsal blood vessel complete, in favorable conditions traceable forward to the brain where it bifurcates — the branches passing ventrally along median faces of circumpharyngeal nervous connectives and reuniting over subpharyngeal ganglion to form the ventral trunk. Subneural trunk, nearly empty throughout in relaxed specimens, probably complete, adherent to parietes. Extra-esophageal trunks pass onto ventral face of gut at 8/9 and continue back into xiii at least, close to median line but without uniting. The trunks are, of course, median to hearts.

Prostates, though reaching through xvii-xix or xx are only medium-sized but apparently normally and fully developed.

Spermathecae, small to medium-sized. The characteristic papilla in an ectal portion of the spermathecal duct easily is disclosed merely by slitting duct open with a needle. Ovaries, fan-shaped, with several egg-strings.

Reproduction. Spermatozoal iridescence, in worms with maximal clitellar tumescence, usually is obvious on male funnels as well as in spermathecal seminal chambers and frequently is brilliant. Iridescence was recognizable on male funnels of four Bombay specimens and in all spermathecal seminal chambers of each specimen. Absence of mature sperm, whenever observed for a number of years, has been attributable to: immaturity, lysis of sperm after the reproductive season had ended, or to virginity. Reproduction, for the present, is assumed to be sexual and biparental. Nevertheless, retention of seminal vesicles in a condition that is juvenile in parthenogenetic forms, and the frequency of inclusion of vesicles in the testis sacs of xi, as in so many forms that are likely to be male sterile, warrant a suspicion that in *posthuma* parthenogenesis may be possible even if only optional as yet.

Abnormality. Left male porophore and prostate lacking in a specimen with an extra genital marking on the right side of xx. Male gonoducts of the left side come to an end in a vesicular widening just in front of 17/18.

Regional homoeosis of some specimens, that has been seen in the past, now is attributable, as in certain lumbricids, to halving of mesoblastic somites early in development.

Remarks. As many as 140 segments have been recorded at some occasion in the past for this species. *P. hupeiensis* which does have as many as 125-140 metameres has been mistaken, several times at least, for *P. posthuma.*

Pattern of genital marking, size, and location, insofar as intrasegmental position (equatorial, slightly median to male pore levels) and regional situation (restricted to segments between xiv and xxx) is concerned, now seems to be unalterable, certainly unchanged in the thousands of specimens that have been examined.

Caecal locations, often difficult to determine, may be able to show whether extra prostates occasionally present in xix are there because of splitting of mesoblastic somites at the 18th level.

P. posthuma obviously is exotic in India in spite of its wide distribution in the north and its commonness in the Gangetic plains. Accidental introduction, presumably by man, may be responsible for its presence in the lowlands of Burma. The original home of the species must be further east, perhaps in Thailand or Indo-China.

Relationships now appear to be closest to *P. fluvialis* Gates, 1939, and *P. juliani* (Perrier, 1875), little known species from Siam and Indo-China.

Table 5

Location of genital markings in Allahabad specimens of *Pheretima posthuma*

On xvii and xix only		1520
Lacking on	left side of xvii	10
	right side of xvii	15
	both sides of xvii	1
	left side of xix	15
	right side of xix	13
	both sides of xix	0
	left side of xvii, both sides of xix	1
Extra marking on	left side of xvi	2
	left side of xx	12
	right side of xx	14
Lacking on	Present on	
Left side of xvii	Left side of xx	6
Right side of xvii	Right side of xx	6
Both sides of xvii	Both sides of xx	2
Right side of xvii	Both sides of xx and xxi	1
Right side of xvii	Both sides of xx	1
Both sides of xvii	Both sides of xx and xxi	1
Both sides of xvii	Right side of xvi, both sides of xx, left side of xxi	1
Left side of xix	Left side of xvi	5
Right side of xix	Right side of xx	1
Right side of xix	Right side of xvi	5
Total		1632

TABLE 6

Typhlosole termination and segment number in Allahabad specimens of *Pheretima posthuma*

Typhlosole ends in segment	Atyphlosolate segments	Number of segments	Remarks
67	12	79	Posterior amputee
79	13+	92+	Young, unsegmented tail-regenerate
88	23	111	
88	24	112	
89	24	113	
90	14	104	Posterior amputee
90	23	113	
90	23	113	
90	24	114	
90	25	115	
90	26	116	
91	24	115	

PHERETIMA RIMOSA Gates, 1931

This species was erected on eight Kengtung specimens with really large seminal vesicles and prostates. Reproduction is assumed to be biparental as sperm had been matured and exchanged during copulation. The types were of an H morph. Records (many of them incomplete) are available now for but 116 specimens. Prostates, in many of the subsequently secured worms, were small or lacking (though ducts were present). Seminal vesicles were small and testis sacs contained only male funnels and discoidal, juvenile, presumably sterile testes. Such worms belonged to parthenogenetic, second-order intermediate morphs. Male porophores and prostatic ducts, in two specimens from To Noi, had almost disappeared. Male gonoducts attenuated posteriorly in forty To Noi specimens in which male porophores and prostatic ducts and male porophores were lacking. Variety *effeminata* was erected on To Noi worms. Two were of late, second-order intermediate morphs. Others were of an R morph. The Latin name is abandoned in favor of more informative terms of reproductive-organ and parthenogenetic polymorphism.

P. rimosa, like *alexandri*, *anomala* and *campanulata*, is a species in which a sperm maturing H morph co-exists along with one or more of the major morphs (A, R, AR, ARZ). Finding of a similar H in other species with advanced major morphs perhaps should be anticipated.

PHERETIMA VIRGO (Beddard, 1901)

This species has been known hitherto only from descriptions of the original seven Siamese specimens. Prostates are small or absent. Spermathecae are vestigial, usually represented only by "extremely small" adiverticulate sacs. A diverticulum, when present, is from the lateral side of the duct and looped. *P. mendosa* Gates, 1932, was erected on 46 Burmese specimens with spermathecal pores, copulatory chambers, stalked glands, genital markings and penes as in *mamillana* but with quite juvenile vesiculae seminalis, small or rudimentary prostates and spermathecae more or less as in *virgo*. Types of *mendosa* and of *virgo*, all sexthecal, belong to parthenogenetic, fourth-order intermediate morphs in which evolution toward an AR morph is well under way. The spermathecae in the sexthecal battery of specimens referred to *P. mamillana* Gates, 1931, were normal, with a looped diverticulum from the lateral face of the spermathecal duct. Prostates appeared to be normal and presumably were functional. Method of reproduction is unknown and information now available as to anatomy provides no clues. As a full complement of normal and apparently functional genital organs is present, *mamillana* must be close to if not actually identical with the biparental H morph from which the *mendosa* and *virgo* lineages have evolved. Both *mamillana* and *mendosa* are suppressed as synonyms of *virgo*. Evolution of polymorphism in *virgo* appears, from the data now available, to be more advanced in a central portion of the range (cf. Table 7) where an A morph has been found and an AR morph may be present.

Classical authorities rarely provided information as to size of spermathecal pores and structure of the spermathecal duct in the musculature of the body wall even when microtome sections had been made. Sometimes, indeed, the pores could not have been seen as they were subsequently found to be elsewhere than as originally stated. Removal of the cuticle often is necessary to permit certain recognition of minute pores, and dissection under a good binocular can provide data that certainly were not obtained from microscope sections. One of the many instances of taxonomic value inhering in previously overlooked organization is the following.

TABLE 7

Number of individuals of various morphs in collections of *Pheretima virgo*

Morphs A	 II	 I_4	 AR	Locality	District	Country
—	2	—	—	Kinmunsakhan	Thaton	Burma
—	1	—	—	Kawkareik	Amherst	
—	11	—	—	Ye		
—	53	—	—	Heimza Basin	Tavoy	
—	251	3	?	Kamaungthwe	Tavoy	
—	203	+	?	Various	Tavoy	
2	1	+	?	Nyaungdonle		
—	111	46	—	Zowai	Mergui	
—	—	7	—	Tale		Siam
—	7	—	—	Kaki Bukit	Perlis	Malay States
—	7	—	—	Baling	Kedah	

A, Athecal morph. H, Hermaphroditic morph with full complement of reproductive organs, presumably normally developed.

I_4, Fourth-order intermediate morphs in which evolution toward an AR morph is under way. AR, Athecal and anarsenosomphic morph. +, Records destroyed. ?, Information presently lacking to permit certain distinction from AR morphs of *campanulata* and *alexandri*. Localities in north-south order.

P. virgo is very close to the *houlleti* group of species. Penial bodies are different from those of the *houlleti* group but have not been seen in full protrusion and need more precise characterization. Differences in size of spermathecal pores and in an ectal portion of the spermathecal duct are invariable. The duct, in each species of the *houlleti* group, narrows considerably within the body wall to open through a minute pore at tip of a very small conical protrusion into a parietal invagination. At copulation, the penis can be inserted only into a small transversely slit-like space. In *virgo*, the spermathecal duct and also its lumen widen considerably within the parietes and the duct opens to the exterior through a large transverse, slit-like aperture. A penis presumably can be inserted much more deeply than in the *houlleti* complex, perhaps far enough to deposit spermatozoa at or close to entrance of the diverticulum where they are to be stored until needed as cocoons are deposited.

PARTHENOGENESIS IN *PHERETIMA*

A characteristic iridescence on male funnels and in spermathecae of earthworms long has been known to indicate, in the first instance, presence of sperm matured by the animal itself, in the second instance, presence of sperm presumably received from another worm during copulation. Examination, some thirty years ago (Gates, 1933) of 250 fully clitellate worms belonging to a single morph of one species and collected during the breeding season showed: That two individuals had produced a little sperm. The others not only had matured no sperm but had no organs in which to receive male gametes should copulation be attempted. Externally adherent spermatophores never were found.

Many endemics, in the monsoon tropics of Asia, breed only toward the end of the rainy season. It was, therefore, comparatively easy, by examination of many specimens collected throughout the breeding season, to determine that sperm probably never are produced by certain forms. The worms are, in fact, male sterile. By isolating anarsenosomphic individuals of *hilgendorfi*, Kobayashi (1937) proved that reproduction is indeed uniparental. Other experiments, except for some preliminary trials mostly with sperm-maturing forms, were prevented by World War II, and since then have not again been attempted.

Meanwhile much information had been accumulated about modifications in genital anatomy associated with male sterility and some of it (taken to India on the last boat to leave Rangoon before Japanese occupation) subsequently was published. Identical changes having been found in different species, a uniform terminology (cf. Gates, 1956) of "reproductive organ polymorphism" became possible. As the same variations were found in the genitalia of other species (cf. Gates, 1954), parthenogenesis could be deduced, even though sperm is matured profusely.

Species of *Pheretima* that are now believed to reproduce parthenogenetically are listed below. Inclusion in the first list does not necessarily mean that every individual of the species reproduces asexually. Nor does it mean that sexual reproduction cannot be obligatory for some individuals of the species. All that can now be said is that individuals do, or the individuals of some morphs must (because of male sterility or organ defects), reproduce parthenogenetically. Genital anatomy of species in the second list provides more or less justification for suspecting or anticipating parthenogenesis. Other names will be added in subsequent publications. Biparental reproduction obviously is not as universal as would have been expected not so many years ago.

Parthenogenesis in species of *Pheretima*

Burma	*Elsewhere*
anomala	agrestis
alexandri	hilgendorfi
campanulata	hupeiensis
diffringens	levis
defecta	
elongata	
exigua	
glabra	
houlleti	
meridiana	
minima	
rimosa	
virgo	
Suspected or anticipated	
bipora	bicincta
birmanica	esafatae
illota	garama
inclara	incongrua
papulosa	montana
pauxillula	pickfordi
robusta	renellana
sulcata	taprobanae
	upoluensis

Testis sacs frequently have been mistaken for seminal vesicles and relationships of sacs with vesicles of xi often have been erroneously characterized. In many such cases vesicles of xi probably are within an unpaired sac or paired sacs. Included vesicles usually are small, juvenile or rudimentary. If enclosure of vesicles by the sacs follows establishment of parthenogenesis, many names may have to be added to the lists. For each of the above taxa there is some additional reason for suspecting parthenogenesis.

DISCUSSION

The variation that has bemused oligochaetologists into erection of unnatural species now can be segregated into five classes.

1) Individual. Species very often were erected on a single type or a short series from a single locality. Even if more material was at hand, information about internal anatomy usually was obtained, perhaps sometimes because of museum regulations, only from one or two dissections supplemented by one or two series of more or less defective microtome sections. Today many of those species still are known only from the original descriptions. Others remain unnatural because all subsequent identifications were of specimens having just those characters recorded for the type or the original lot. More or less variant specimens, especially when from a distant locality, became types of other "species." Recent studies of Burmese and other oriental earthworms (also cf. Gates, 1957, for a similar finding in the Lumbricidae) have shown that characters by which species were defined often are among those most liable to individual variation. Twelve names, two in current use, are now known (Gates, in MS) to be synonyms of one widely distributed form. In contrast to possessors of many names are the congeries or complexes masquerading as species, presumably because important differences were attributed to varietal or individual variation. Especially regretted, in case of little known species, possibly on the way to extinction, is the failure to publish information about variation that must have been noticed while identifying worms for regional or population studies.

2) Anomalous. One sort results from modification of embryonic development presumably often induced (Gates, 1958) by environmental factors. *Allolobophora relicta* of the Lumbricidae is an illustration of a "species" erected on a type which can, with some justification, be called monstrous. Other sorts of anomalies result from presence of one or more of the kinds of parasites by which earthworms are infested often in large numbers.

3) Regenerative. Almost any species seems to be liable to more or less frequent loss of a taxonomically critical anterior portion of the body or some fraction of it. Restoration of the lost part, not exactly duplicated, and especially in case of a single specimen from a little known area, is believed to have enabled erroneous characterization of several species never since recognized. Probability of such error is greatest in genera like *Perionyx*, all species of which may have a high regenerative

capacity. This enables replacement of any portion of the pre-intestinal region or regeneration of a head (containing all organs of the pre-intestinal region) at any level except those way back in a small posterior section of the body. The diversity of structure after regeneration is now known to be so great that no two regenerates are likely to be identical even when produced at the same level and in the same conditions. Regeneration homoeotics are frequent and probably have not always been recognized as such.

4) Geographic. This sort of variation is, of course, not shown by the better known peregrine forms that have been transported by man throughout the world. Intensive studies of an areal fauna when made locally, as in South Africa (Pickford, 1937) and Burma, have revealed geographical races in various endemics. These, apparently, will have to be studied in recently unglaciated areas where the soil and other earthworm habitats remain less influenced by human activities. Considerable local collecting in areas such as New Guinea may be necessary before subspecies can be distinguished from species.

5) The variation that is now known to be possible after reproduction has become parthenogenetic. This method of reproduction permits, in subspecies as well as in species, evolution of numerous clones or morphs. Whether all of the specific names based on defective individuals of the more aberrant morphs ever can be placed with certainty in any synonymy now seems doubtful. Some anatomical modifications of the morphs also were made during evolution of various species. The reproductive system presently appears to be the only one that is changed during parthenogenetic evolution. Hence, the characterization of "reproductive organ polymorphism" which can be shortened to parthenogenetic polymorphism or even to genital polymorphism if parthenogenesis is understood to be basic.

The new systematics provides no criteria for species in animals that reproduce asexually. In earthworms, parthenogenetic strains now appear to have evolved recently from sexual forms presumably definable in accordance with ultra-modern requirements. Proof of the descent is provided, in better known cases, by intermediates linking even the most modified morphs to one that is normally hermaphroditic and sperm producing. Instances also are known in which adults of a male sterile morph are distinguishable from sexual worms only by the juvenile condition of their testes and other male organs. If considerable proportions of the earthworms in various regions of the world are not to be left in an "ataxic" limbo as it were, species must be more than an interbreeding population, even in that far distant future when limits of interbreeding among these soil dwellers will have been discovered. A species, as understood herein, includes any population that meets breeding requirements and also all recently evolved strains, clones, morphs, that can be linked by intermediate stages to the sexual population.

The classical system of the Oligochaeta, regardless of original intention, eventually crystallized around two suppositions. 1) That genera and higher categories can be defined and arranged in straight-line phylogenetic sequences by a very few and often quite simple or generalized characters. 2) That other differences in structure (including all of the vascular and nervous systems) are phylogenetically meaningless and hence of little or no taxonomic importance.

Assumptions basic to the author's revisions of that system can be stated somewhat as follows: A species cannot be finally defined until extent of its individual and geographic variation throughout the entire range is known. (Obviously, then, for some time to come, definitions must be changed as more data become available.) Any generic definition necessarily is tentative and liable to modification until such time as all extant species have been found and finally defined. Species so closely related as to belong in a monophyletic genus should prove the relationship by a considerable amount of over-all anatomical similarity. Genera so related as to belong together in a subfamily still should have some anatomy in common. Species rather generally are distinguished by characters of systems most liable to rapid evolutionary modification. Genera are to be defined by characters less liable to change, subfamilies by others still more conservative.

The study of individual, anomalous and regenerative variation, as well as of genital and geographical polymorphism, shows conclusively that in earthworms the reproductive system is by far the most liable to rapid evolutionary modification.

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MIDDLE TRIASSIC NAUTILOIDS FROM SINAI, EGYPT, AND ISRAEL

By Bernhard Kummel

WITH FOUR PLATES

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No. 7 — Middle Triassic Nautiloids from Sinai, Egypt, and Israel

By Bernhard Kummel

Triassic formations and faunas from the southern part of Tethys in the Middle East are as yet very incompletely known. Localities with Triassic formations have been recognized to the northeast of the Dead Sea in Jordan, in the Negev of southern Israel and in Sinai, Egypt (Fig. 1). This particular study is concerned with a small fauna of nautiloids from Araif-el-Naga, Sinai, and the Makhtesh [= Wadi] Ramon, Israel. Some of the Sinai specimens are those recorded but not described by Awad (1945) and which are deposited in the British Museum (Natural History). These specimens were obtained on loan through the courtesy of Dr. M. K. Howarth of that institution. A second collection consisting of many, but generally poorly preserved, specimens from Araif-el-Naga, Sinai, and from Makhtest Ramon, Israel, have been presented to the Museum of Comparative Zoology by the Iraq Petroleum Company, Ltd., through the courtesy of Dr. R. G. S. Hudson. Finally, a third group of five specimens from the Makhtesh Ramon was obtained on exchange with Mr. A. Parness of the Israel Geological Survey.

The existence of Triassic strata in Israel was first discovered by the geologist of the Iraq Petroleum Company whose work was partially published by Shaw (1947). These Triassic strata were found in the Makhtesh Ramon where they crop out in the center of a large anticlinal structure. Brief notes on some vertebrate fossils from these exposures have been published by Swinton (1952) and Brotzen (1955). Recently, Brotzen (1957) has described more vertebrate remains plus some pelecypods from Makhtesh Ramon. A significant part of this paper (Brotzen, 1957) is a clear discussion of the stratigraphy of the Triassic strata exposed in the Makhtesh Ramon with data on the distribution of fossils in this section. Brotzen's stratigraphic section of the Triassic formations exposed in the Makhtesh Ramon is as follows:

Member "D", the *Ceratites* beds		
30.	Limestone and marls with *Ceratites* (*Ceratites*, zone 5)	2.0 m
29.	Limestone and marls with *Ceratites* (*Ceratites* zone 4)	5.8
28.	Light brown marls and limestones with *Ceratites*, *Arcestes*, *Joannites*, *Placodus*, *Nothosaurus* (Ceratites, zone 3)	5.0
27.	Hard limestone layers	2.4

26.	Limestone and marls with *Paraceratites* spp., abundant nautiloids, pelecypods (*Ceratites* zone 2)	13.0
25.	Terebratula layer	0.10-0.40
24.	Sandy limestone, bluish, and shales with bone beds, *Paraceratites*, *Psephosaurus picardi* (Brotzen, 1957) *Nothosaurus*, *Myophoria laevigata* Goldfuss, *Mysidia*, *Lithophagoides*, *Coenothyris vulgaris* Schlotheim, *Pleuromya elongata* Schlotheim, aff. *Homomya* (*Anoplophora*) *fassaensis* Wissmann, nautiloids (*Ceratites* zone 1)	6.0
23.	Sandy and shaly layers	1.8

Member "C", the reef beds

22.	Sandstone	1.1
21.	Tan, pink, and blue shale with fish remains, bones, *Lingula*	2.4
20.	Ash	1.2
19.	Brown and gray laminated shale, sandy at the top; fish teeth, plant remains	16.6

Member "B", the *Beneckeia* beds

18.	Marls, light yellow and brown. *Beneckeia* sp. 3, *Myalina* spp., bones	6.0 m.
17.	Sandstone	0.3
16.	Shale, dark-green, *Beneckeia* sp. 3, *Beneckeia* sp. 2, *Myalina* spp., bones	5.0
15.	Shales with sandy layers containing *Beneckeia* sp. 3, *Beneckeia* sp. 2, *Myalina beneckei*, *Myalina* spp., bones	2.5
14.	Porphyritic sill (locally)	
13.	*Myalina* beds with bones	0.3
12.	Shales, greenish, *Psephosaurus* beds	6.0
11.	*Myalina* limestone	0.2
10.	Marls with rich fauna, *Beneckeia* sp. 2, *Myophoria* sp., brachiopods, bones	2.0
9.	Sandstone with trails	0.3
8.	Shales with *Myalina*, *Myophoria*, bones	4.0
7.	Sandstone with *Beneckeia*, sp. 1	0.3
6.	Brownish shales	1.5

Member "A", wood-bearing beds

5.	Dark grey, hard, igneous rocks, probably of felsitic affinities—locally absent	
4.	Sandstone	2.5
3.	Green-grey, also tan, laminated shale, *Lingula*	4.3
2.	Brown sandstone, interbedded with grey shales; *Lingula*, fish teeth, plant remains, bone fragments	3.2
1.	Grey laminated medium hard shale, with badly preserved fossils	6.4

As can be seen from this section ammonoids are well represented and a monograph on a part of this fauna by Mr. A. Parness is now in preparation. Preliminary analysis of the fauna from the Makhtesh Ramon enabled Brotzen to conclude that *Ceratites* zones 3 to 5 of member "D" were most likely lower Ladinian in age; that member "C" and *Ceratites* zones 1 to 2

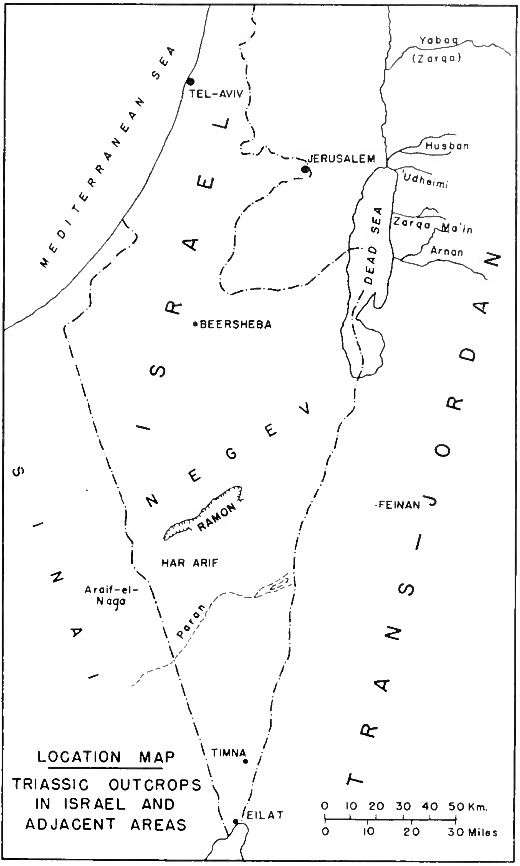

Figure 1. Location map of Triassic outcrops in Israel and adjacent areas. A glossary of the Hebrew, Arabic, and English names most commonly used on maps of this area can be found in Ball and Ball (1953, p. 111).

were Anisian in age (Paraceratitan age of Spath); that the *Beneckeia* zones were lower Anisian and possibly also in part uppermost Scythian in age; and finally that Member "A" was Scythian for which, however, there is no paleontological evidence. These age assignments appear to be correct. Nautiloids are present in member "B" (the *Beneckeia* beds) and in member "D" (the *Ceratites* beds). The only nautiloids available in the present collection from member "C" (*Beneckeia* beds) is *Indonautilus awadi* n. sp. Member "D" (the *Ceratites* beds) contains *Germanonautilus bidorsatus* (Schlotheim), *G. salinarius* (Mojsisovics), *Mojsvaroceras* cf. *marloti* (Mojsisovics), and *M.* sp. indet.

The only Triassic formations known in Egypt crop out in the Gebel Araif-el-Naga, Sinai, in the center of a large dome. A brief study on the stratigraphy and fossils from these Triassic formations has been published by Awad (1945). The oldest strata exposed in the Araif-el-Naga dome are vari-colored unfossiliferous sandstones of unknown thickness. These strata are overlain by 20-25 meters of thin-bedded limestones, sandstones, shales, gypsums, and marls. Within this series there are a number of fossiliferous bands from which Awad (1945) identified the following species:

Enantiostreon difformis (Schlotheim)
Enantiostreon spondyloides (Schlotheim)
Myophoriopsis (*Pseudocorbula*) *subundata* (v. Shauroth)
Pecten (*Pseudomonotis*) *inequistriatus* Münster
Pecten (*Syncloncma*) *discites* Schlotheim
Plicatula (*Pseudoplacunopsis*) *fissistriata* Winkler
Modiola raibliana Bittner
Schafhautlia sp.
Omphaloptycha gregaria Schlotheim
Nucula subequlatera Schafhautl
Leda elliptica (Goldfuss)
Pteria aff. *cassiana* Bittner
Myophoria elegans Dunker
Myophoria cardissoides (Schlotheim)
Myophoria germanica Hohenstein
Myophoria coxi Awad
Myophoria laevigata (Zieten)
Anodontophora munsteri Wissmann

A unit of approximately five meters in thickness in the mid part of this 20-25 m. unit contains, according to Awad, numerous nautiloids and ammonoids. Several specimens of cephalopods were submitted by Awad to L. F. Spath who reported (in Awad, p. 425) that the majority of the ammonites were *Ceratites*, most comparable to the group of *C. flexuosus* and probably deserving a separate subgeneric name. Spath likewise considered these ammonoids as indicating a lower Ladinian age. A fragment of a *Beneckeia* was also recognized by Spath in Awad's collection. The writer's specimens of nautiloids from the Sinai presumably came from this fossiliferous unit and include *Germanonautilus* cf. *adrena* (Fritsch), *Mojsvaroceras* cf. *marloti* (Mojsisovics), and *Indonautilus awadi* n. sp.

Above this fossiliferous unit there are 25 meters of greenish and yellowish clays, shales, and marls with thin beds of limestone. From this unit Awad (1945) recognized *Pecten* (*Syncloнema*) *discites* Schlotheim, *Hoernesia* cf. *hebanensis* Cox, *Omphaloptycha gregaria* Schlotheim, and fragments of nautiloids. The uppermost unit of the Triassic sequence consists of 50-60 meters of massive, hard, limestone, probably dolomitic, devoid of fossils.

Awad is not clear as to the stratigraphic position of his specimen of *Beneckeia* identified by Spath, but it seems doubtful that it is from the same unit as his *Ceratites*. As noted above, Spath came to the conclusion that the ammonites indicated these deposits were lower Ladinian in age, but Awad on the basis of his study of the remainder of the fauna favored a lower Anisian age. This conflict of opinions cannot be adjusted until the position of *Beneckeia* relative to the other ammonoids is precisely known. On this question Brotzen (1957, p. 207) assumed that equivalents of his *Beneckeia* beds must be present in the Araif-el-Naga dome and that the main fossiliferous beds were equivalent to his member "D" (the *Ceratites* beds).

The few other areas of Triassic exposures in the Middle East are either poor or totally lacking in cephalopods. The only other area of Triassic exposures in Israel is at Har Arif, 20 km. southwest of Makhtesh Ramon, where Bentor and Vroman (1952) identified a sequence comparable in lithology and fossil content to that of Makhtesh Ramon but no details are available.

Cox (1932) has recognized a Lower Triassic fauna from shale and sandstone beds exposed along the eastern shore of the Dead Sea in the neighborhood of Wadi Zarqa Mai'n (Fig. 1). This fauna includes *Pseudomonotis* (*Claraia*) *aurita* (Hauer), *My-*

ophoria laevigata (Zieten), *Myophoria praeorbicularis* Bittner, *Anodontophora fassaensis* (Wissmann), and *Lingula tenuissima* Bronn. Another Triassic fauna from Jordan is known from the region of Wadi Husban at the northeast corner of the Dead Sea (Fig. 1). In this fauna Cox (1932) recognized a large number of species of pelecypods, a few species of brachiopods and gastropods, one nautiloid (*Pleuronautilus* sp.) and one ammonoid (*Beneckeia* sp.). In his first study of this fauna, Cox (1924) concluded that it was most probably Karnian in age. Determination of the age of this fauna was complicated by the mixture of Alpine and Germanic species. In a subsequent study based on additional material from the same localities Cox (1932) withdrew his conclusion as to the age of the fauna and left the problem of age open. Part of the pelecypod fauna appears to indicate an Upper Triassic age, but these forms are associated with the ammonoid *Beneckeia* sp. which suggests a Lower Muschelkalk (Anisian age) as do some of the brachiopod and pelecypod species.

These few areas of Triassic formations in Jordan, Israel, and Sinai, in their stratigraphy and facies development, indicate approximation to the southern shores of Tethys. Recently Avnimelech (1959) has reported on a deep well drilled at Kfar Yeruham (Rekhme) situated approximately 30 km. south of Beersheba and 40 km. north of the Ramon anticline. The cuttings from 2217 to 2760 m. consist of black bituminous-pyritic shale and coarse, granulous detrital limestone. The samples from 2650 m. included an ammonite identified by Avnimelech as the inner whorls of a *Beneckeia;* in addition this sample contained *Myophoria elegans* or *postera* and *Dielasma ecki* indicating an Anisian age. Samples from 2235-2576 m. possibly contain *Halobia*, suggesting an Upper Triassic age (Karnian). The lithology of the Triassic strata in this bore hole indicates a more pelagic facies than encountered in the outcrop area of Triassic formations from the Dead Sea to the Sinai. On the basis of this data, Avnimelech (1959, p. 174) has constructed a highly interesting paleogeographic map for the Middle Triassic. Following along the southern regions of Tethys, the next area of Triassic exposures to the east is in central Saudi Arabia (Arkell, et al., 1952; Steineke, et al., 1958); to the west the first Triassic exposures are at Azizia 40 km. south of Tripoli, Libya (Coggi, 1940).

SYSTEMATIC DESCRIPTIONS

Family TAINOCERATIDAE Hyatt, 1883

Genus GERMANONAUTILUS Mojsisovics, 1902

Type species. Nautilus bidorsatus Schlotheim, 1832.

The largest number of specimens in this collection of nautiloids are species of the genus *Germanonautilus*. Unfortunately, they are generally the most poorly preserved and only a small series of them are sufficiently well preserved to warrant detailed discussion. Specimens from the Middle Triassic strata at Makhtesh Ramon, Israel, can be assigned to *Germanonautilus bidorsatus* and *G. salinarius*. A large living chamber with only two or three camerae of the phragmocone appears to belong to, or is at least closely related to, *Germanonautilus advena* Fritsch (1902, pl. 2, figs. 10, 11). This particular species of *Germanonautilus* has the most depressed whorl section of all the species assigned to this genus and for this reason is quite distinctive.

Fourteen species of *Germanonautilus* are known to date ranging from the Scythian into the Karnian. The genus is particularly widespread in the Muschelkalk facies of Germany.

GERMANONAUTILUS SALINARIUS (Mojsisovics)

Plate 3, figures 1, 2

Nautilus salinarius Mojsisovics, 1882, p. 282, pl. 91, fig. 3; Hauer, 1887, p. 13; Hauer, 1892, p. 253; Hauer, 1896, p. 243; Diener, 1900, p. 36.

Nautilus f. indet. Mojsisovics, 1882, p. 282, pl. 92, figs. 1a-b.

Germanonautilus cf. *salinarius*, Diener, 1907, pp. 29-30, pl. 3, fig. 1.

Germanonautilus salinarius, Diener, 1915, p. 330; Alma, 1926, p. 114; Kummel, 1953, p. 28, fig. 9 A.

Germanonautilus sp. ind. aff. *salinario*, Diener, 1915, p. 330 (for *Nautilus* f. indet. Mojsisovics, 1882, p. 282, pl. 92, figs. 1a-b).

Two of the specimens from Makhtesh Ramon can be assigned to this common Tethyan species of *Germanonautilus*. The larger and best preserved specimen measures 91 mm. in diameter, 66.7 mm. for the width of the last whorl, 53.0 mm. for the height of the last whorl, and the umbilicus is 14.0 mm. in diameter. The second specimen is a phragmocone of 68 mm. in diameter but not well preserved.

The conch is moderately involute with a robust, subquadrate whorl section. The whorl sides are slightly arched and converge toward a broad, flattened venter. The ventral and umbilical shoulders are well rounded. The umbilical wall is broadly arched and slopes at a fairly steep angle to the umbilical seam. The suture is simple, being characterized by shallow ventral and lateral lobes. The siphuncle is subcentral, being closer to the dorsum than to the venter.

Remarks. Of all the specimens which have been assigned to this species that figured by Mojsisovics (1882, pl. 92, figs. 1a-b) is most similar to the Israeli specimens recorded here. The type specimen of *G. salinarius* (Mojsisovics, 1882, pl. 91, figs. 3a-b) is more quadrate in whorl section, the whorl sides converging very gently toward the broad venter. Mojsisovics' other specimen and the Israeli specimen display more convergence of the whorl sides but this is not considered to be of specific importance, the difference being much too slight and only that to be expected. The specimen from the Himalayas described by Diener (1907) is also nearly identical to the Israeli specimens. Diener (1907) makes note of the presence of an annular lobe on his Himalayan specimen, a feature which is also present on the Israeli specimen, even though weakly. This feature, however, was not observable on the Alpine specimens.

Occurrence. Middle Triassic, *Ceratites* beds, Makhtesh Ramon, Israel.

Repository. MCZ 6090 (Pl. 3, figs. 1, 2); MCZ 6091, unfigured specimen

GERMANONAUTILUS BIDORSATUS (Schlotheim)

Plate 3, figures 3, 4

Nautilus bidorsatus Schlotheim, 1832, p. 82, pl. 31, figs. 2a-b (*non* 2c); Bronn, 1837, p. 177, pl. 11, fig. 21; Mallada, 1880, p. 243, pl. 1, figs. 1-2; Rassmuss, 1915, p. 286.

Temnocheilus bidorsatus, Foord, 1891, p. 160; Franz, 1903, p. 494.

Germanonautilus bidorsatus, Mojsisovics, 1902, p. 235; Diener, 1915, p. 329; Kieslinger, 1925, p. 120, text-fig. 8; Schmidt, 1928, p. 285; text-figs. 788, 790; Kutassy, 1933, p. 712; Kummel, 1953, p. 28.

This well known species of *Germanonautilus* is represented by a well preserved partial phragmocone of slightly less than one-half volution. The ventral and umbilical shoulders of the specimen are rounded, the whorl section being broader than high. The venter is broadly sulcate and the umbilical walls arched. The published illustrations of *G. bidorsatus* leave much to be desired and in the identification of this specimen the writer was greatly aided by a splendid collection of specimens from the Muschelkalk of Germany in the Museum of Comparative Zoology. The Israeli specimen, as far as can be told, is nearly identical to the specimens from Germany and should be assigned to *G. bidorsatus*. In addition to this specimen there is also a very poorly preserved complete phragmocone.

Occurrence. Middle Triassic *Ceratites* Beds, Makhtesh Ramon, Israel.

Repository. MCZ 6092 (Pl. 3, figs. 3, 4); MCZ 6093, unfigured specimen.

GERMANONAUTILUS cf. ADVENA (Fritsch)

Monilifer (= *Germanonautilus*) *advena* Fritsch, 1902, pl. 2, figs. 10-11.
Germanonautilus advena (Fritsch), Kummel, 1953, p. 28.

A poorly preserved specimen consisting of the living chamber and three camerae deserves at least a brief mention due to its extremely depressed whorl section. Whorl sections such as this are not common among the known species of *Germanonautilus* and is characteristic only of *G. advena* (Fritsch). The whorl section of the present specimen measures approximately 90 mm. in width and 50 mm. in height. Measurements of Fritsch's figured specimen (Fritsch, 1902, pl. 2, fig. 10) yield 70 mm. for the width of the whorl and 38 mm. for the height. The percentage of width to height is approximately the same. The present specimen differs from *G. advena* mainly in the less convergent aspect of the whorl sides and the broadly arched umbilical slope rather than a roughly straight slope as in *G. advena*.

Occurrence. Middle Triassic formation at Araif-el-Naga, Sinai, Egypt.

Repository. MCZ 6094.

Genus MOJSVAROCERAS Hyatt, 1883

Type species. Temnocheilus neumayri Mojsisovics, 1882

MOJSVAROCERAS cf. MORLOTI (Mojsisovics)

Plate 1, figures 6-8; plate 2, figures 1-6

Temnocheilus morloti Mojsisovics, 1882, p. 268, pl. 88, fig. 3; Hauer, 1896, p. 248.
Mojsvaroceras morloti, Mojsisovics, 1902, p. 233; Diener, 1915, p. 334; Gugenberger, 1927, p. 102, Kutassy, 1933, p. 718.
Metacoceras (*Mojsvaroceras*) *morloti*, Kummel, 1953, p. 21.

Several specimens of variable preservation that appear to be conspecific are in the collections from Makhtesh Ramon, Israel, and Araif-el-Naga, Sinai, Egypt. The best preserved example is a phragmocone illustrated on Plate 2, figures 1, 2. It measures 67.8 mm. in diameter, 30.7 mm. in height of last whorl, 40 mm. in width of the last whorl, and the umbilicus measures 18 mm. in diameter. The largest example (MCZ 6097), also a phragmocone, is weathered and generally not as well preserved but it measures 73.5 mm. in diameter, 51.3 mm. for the width of the last whorl, 35.0 mm. for the height of the last whorl, and 21.3 mm. for the diameter of the umbilicus. The whorl section is subquadrate with a broad, low arched venter, rounded ventral shoulders, flattened lateral areas, rounded umbilical shoulders and a fairly broad sloping umbilical wall. The suture consists of shallow ventral and lateral lobes. The phragmocone is smooth, except for fairly large low nodes on the umbilical shoulder. There appear to be 10 such nodes on this specimen.

A smaller conspecific specimen from the same locality and horizon as that described above is illustrated on Plate 2, figures 3-6 (MCZ 6096). This specimen measures 37.0 mm. in diameter, 24.6 mm. in width of the last whorl, 18 mm. in height of last whorl, and 8.5 mm. for the diameter of the umbilicus. The whorl section is more trapezoidal in outline than the larger more mature specimen, with the lateral areas distinctly converging toward the venter. Likewise, the ventral and lateral lobes are slightly deeper and there is an annular lobe. The small umbilicus is subcentral in position, that is, closer to the dorsum than the venter. The ventral shoulders are smoothly rounded but the umbilical shoulders are sharply rounded. The first volution of this specimen is illustrated on Plate 2, figure 6 and measures 25.5 mm. in diameter. At the end of the first volution the whorl section measures 17.4 mm. in width, 12 mm. in height, and the umbilicus is 5 mm. in diameter. The ventral half of the first half whorl is broken so that a portion of the siphuncle is exposed. This is typically beaded, composed of slender cylindrical sections with marked constrictions between each of the segments. The shell is preserved on parts of this small specimen and has rather marked and coarse growth lines that inscribe a deep hyponomic sinus on the venter. The nodes which are so conspicuous on the larger specimens are absent on the smaller specimen.

The specimens discussed above came from Middle Triassic strata at Makhtesh Ramon, Israel. An additional small, immature specimen from Araif-el-Naga is tentatively considered to be conspecific with this species and is illustrated on Plate 1, figures 6-8. This specimen measures 27.5 mm. in diameter, 20 mm. in the width of the last whorl, 14 mm. in the height of the last whorl, and 6.3 mm. in diameter of the umbilicus. The shape and general character of the conch is similar to that of the specimen described above and illustrated on Plate 2, figures 3-6, except that the position of the siphuncle is central and the annular lobe is only weakly developed. More of the shell is preserved on this specimen and it bears on the most adoral part of the outer volution fine growth lines with a deep tongue-shaped sinus on the venter which in places is also reflected on the internal mold. The shell on the earliest volution has a fine reticulate ornamentation (Pl. 1, fig. 7).

Remarks. Evolute nautiloids with subquadrate whorl sections and nodes on either or both of the shoulders form one of the most common and widespread types found in late Paleozoic and Triassic formations. The late Paleozoic species comprise the genus *Metacoceras* for which about 50 species have been described. The Triassic representatives are nearly identical to the late Paleozoic *Metacoceras* and differ mainly in a slightly greater involution and the presence of an annular lobe. Because of this close relationship, *Mojsvaroceras* has been considered to be a subgenus of *Metacoceras* (Kummel, 1953, pp. 19-23). At present there are 18 described species of the subgenus *Mojsvaroceras* known from the region of the Tethyan geosyncline, northern Siberia, and western United States (Idaho and California). Stratigraphically, two of these species are known from Scythian strata, 12 from the Anisian, one from the Ladinian, and three from the Karnian. The species of *Mojsvaroceras* are differentiated on slight differences in the shape of the whorl section and the disposition of the nodes. As is typical of Mesozoic nautiloid faunas, large samples of any of these species are not known or available and the range of intra-specific variation poorly understood. For this reason the specimens described here are not given a new specific name but rather assigned to an already described species which it most closely resembles. The type of *Mojsvaroceras morloti* (Mojsisovics, 1882, p. 268, pl. 88, fig. 3) differs from the Middle East specimens described here merely in the greater breadth of the outer whorl but otherwise is nearly identical.

Occurrence. Plesiotypes (Pl. 2, figs. 1-6) and unfigured specimen from Middle Triassic formations at Makhtesh Ramon, Israel; Plesiotype (Pl. 1, figs. 6-8) from Middle Triassic at Araif-el-Naga, Sinai, Egypt.

Repository. Plesiotype (Pl. 2, figs. 1, 2) MCZ 6095; Plesiotype (Pl. 2, figs. 3-6) MCZ 6096; Plesiotype (Pl. I, figs. 6-8) BM (NH) C 55325, unfigured specimens MCZ 6097, MCZ 6098.

MOJSVAROCERAS n. sp. indet.

Plate 2, figures 7, 8; plate 4, figures 3, 4

A single, incomplete phragmocone from Makhtesh Ramon, Israel, is clearly a species of *Mojsvaroceras* but quite different from *Mojsvaroceras* cf. *morloti* which is also recorded from this area. It is only because of the incompleteness of the specimen that the author refrains from proposing a new name.

The specimen measures 67 mm. in diameter and consists of only a half volution of the conch, all septate. The cross-section of the most adoral part of outer whorl is subquadrate, having subparallel lateral areas and a broadly arched venter. Both the ventral and umbilical shoulders are rounded and the umbilical wall is broadly arched and nearly vertical. The quadrate aspect of the whorl section is apparent only on the most adoral portion of the specimen; prior to this the whorls are depressed, elliptical in shape. The innermost whorls visible are almost circular in cross-section.

The whorl sides bear large blunt nodes along the ventral shoulder which are slightly elongated in a dorsoventral direction. On the earlier volutions where the whorl section is depressed and elliptical in cross-section, the large nodes are at the mid-region on the flanks at a position where both the umbilical and ventral shoulders begin. As the whorl section becomes more quadrate in cross-section the nodes shift toward the ventral shoulders.

The siphuncle is in an extreme dorsal position and measures 3.5 mm. in diameter.

The suture is of a very simple pattern having a broad, shallow lobe on the flanks and passing over the arched venter in nearly a straight line.

Two small, fragmentary specimens from Araif-el-Naga, Sinai, are believed to be conspecific with the larger form from Makhtesh

Ramon, Israel. The better preserved of these specimens is illustrated on Plate 2, figures 7, 8. This specimen consists of slightly more than one-third of a volution of phragmocone. The most adoral camerae are depressed, elliptical in cross-section, having a broadly arched venter, arched whorl sides and umbilical wall. Blunt nodes are present on the ventral shoulder. The suture has a very slight lateral lobe and passes over the venter forming a very slight ventral saddle. The siphuncle is subcentral in position. This small specimen differs from the larger example only in the lesser prominence of the lateral nodes.

Remarks. The changes in the cross-section of the whorls during the ontogeny of this species and the large lateral nodes are the distinctive features that separate this species from all others of *Mojsvaroceras* that have been recorded to date. Of the seventeen species of *Mojsvaroceras*, fourteen are confined to Tethys, and of these twelve are known only from the general area of the Alps and two from the Himalayas. Of all these species only *M. binodosum* (Hauer) has at least some resemblance in gross conch features to *Mojsvaroceras* n. sp. indet. but that species as the name implies has nodes both on the ventral and umbilical shoulders. Likewise the nodes seem to disappear adorally and are absent on the living chamber. The other alpine species differ even more in whorl shape and pattern of ornamentation. There is likewise no resemblance to *M. nivicola* Diener or *M. kagae* Diener from Anisian strata of the Himalayas.

Occurrence. Middle Triassic formations at Araif-el-Naga, Sinai, Egypt, and from *Ceratites* beds (probably higher part) at Makhtesh Ramon, Israel.

Repository. Pl. 4, figs. 3, 4, MCZ 6099; Pl. 2, figs. 7, 8, MCZ 6100.

Family LIROCERATIDAE Miller and Youngquist, 1949

Genus INDONAUTILUS Mojsisovics, 1902

Type species. Nautilus kraffti Mojsisovics, 1896

Indonautilus is one of a large group of Triassic nautiloid genera which are either monotypic or have few species. The genotype is known from a single specimen from the *Halorites* limestone (Norian) at Bambanag in the Himalayas. In addition, Jaworski (1915, pp. 131-132) has assigned to the type species a specimen from Norian rocks on the Island of Misol. A new species of *Indonautilus* is now recognized among the collections from the Sinai and Israel. *Indonautilus* is characterized by its extremely involute conch, whorl section with sharply to acutely rounded ventral shoulders, broadly flattened venter, and absence of an annular lobe. On the basis of this morphological framework it appears most likely that *Indonautilus* is closely related to and derived from *Paranautilus*.

INDONAUTILUS AWADI n. sp.

Plate 1, figures 1-5; plate 2, figures 9, 10; plate 4, figures 1, 2.

Four specimens from Araif-el-Naga, Sinai, and one from Makhtesh Ramon are available for study. The holotype specimen (BM (NH) C 55324, Pl. 1, figs. 1-3) measures 72.0 mm. in diameter and is all phragmocone, as are all the specimens in the collection. The holotype has a tightly coiled conch with no umbilical opening, the whorl section is subquadrate measuring 45 mm. in height and 42 mm. in width. The flanks converge slightly toward the venter and are only weakly arched; the venter is broad and flattened. The ventral shoulders are sharply rounded. The suture forms a broad shallow ventral lobe, a lateral lobe that occupies the lower two-thirds of the flanks and a broad low saddle that occupies the upper third of the flanks. There does not appear to be any annular lobe. The siphuncle is slightly dorsal of a central position.

The specimen illustrated on Plate 1, figures 4, 5 is thought also to be a representative of this species. The position of the siphuncle, degree of involution, degree of compression of the whorl section and the suture suggest this relationship. At first glance the most noteworthy difference is the lack of sharply rounded ventral shoulders. However, the specimen is an internal mold (all phragmocone) that has undergone much weathering which masks the details, namely the more rounding of the whorl section especially in the region of the venter. This particular specimen appears to be identical with that figured by Awad (1945, pl. 3, figs. 22a, b) from the same horizon and locality. The main features of the conch of immature forms are illustrated by the specimen shown on Plate 2, figures 9-10.

The specimen from Makhtesh Ramon, Israel (Pl. 4, figs. 1, 2), measures 80 mm. in diameter, approximately 64 mm. for the width of the last whorl, and 53 mm. for the height of the last whorl. It is believed to be conspecific with the specimen from

Sinai even though it differs in some features. For one thing the ventral shoulders of the Israeli specimen are not so sharply rounded. The venter also is slightly arched rather than being flattened. Another striking difference is the great width of the most adoral camerae; however, the great expansion of the whorl width is developed by the most adoral six camerae. Prior to these last six camerae, the conch dimensions are comparable to those on the holotype. In other features such as the degree of involution, position of the siphuncle, and the suture, the Israeli specimen is nearly identical to those from Sinai.

Remarks. *Indonautilus awadi* is characterized by its occluded conch, sharply rounded ventral shoulders, and its suture. *Indonautilus kraffti* is slightly more evolute and the suture is not quite so sinuous. The two specimens of the type species that have been recorded to date are likewise considerably smaller than the specimens from the Sinai and Israel.

Occurrence. Middle Triassic at Araif-el-Naga, Sinai, Egypt, and from *Beneckeia* beds at Makhtesh Ramon, Israel.

Repository. Holotype (Pl. 1, figs. 1-3) BM (NH) C 55324; paratype (Pl. 1, figs. 4-5) BM (NH) C 55321; paratype (Pl. 2, figs. 9-10) BM (NH) C 55322; unfigured paratype BM (NH) C 55323; paratype from Israel (Pl. 4, figs. 1, 2) MCZ 6101.

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PLATES

PLATE 1

Figures 1-3. *Indonautilus awadi* n. sp. Holotype, BM (NH) C 55324, from Middle Triassic at Araif-el-Naga, Sinai, Egypt. X 1.

Figures 4, 5. *Indonautilus awadi* n. sp. Paratype, BM (NH) C 55321, from Middle Triassic at Araif-el-Naga, Sinai, Egypt. A weathered immature specimen. X 1.

Figures 6-8. *Mojvarroceras* cf. *morloti* (Mojsisovics). BM (NH) C 55325, an immature specimen from Middle Triassic at Araif-el-Naga, Sinai, Egypt. X 1.

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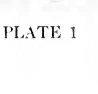

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PLATE 1

PLATE 2

Figures 1-6. *Mojsvaroceras* cf. *morloti* (Mojsisovics). From Middle Triassic at Makhtesh Ramon. 1-2, MCZ 6095; 3-6, MCZ 6096. X 1.

Figures 7-8. *Mojsvaroceras* n. sp. indet. MCZ 6100, from Middle Triassic at Araif-el-Naga, Sinai, Egypt. X 1.

Figures 9-10. *Indonautilus awadi* n. sp. BM (NH) 7 55322, immature specimen from Middle Triassic at Araif-el-Naga, Sinai, Egypt. X 1.

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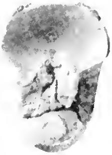

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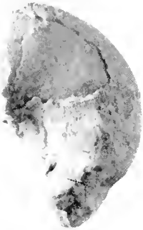

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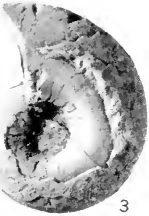

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PLATE 2

PLATE 3

Figures 1-2. *Germanonautilus salinarius* (Mojsisovics). MCZ 6090, from Middle Triassic *Ceratites* beds, Makhtesh Ramon, Israel. X 1.

Figures 3, 4. *Germanonautilus bidorsatus* (Schlotheim). MCZ 6092, from Middle Triassic *Ceratites* beds, Makhtesh Ramon, Israel. X 0.5.


3


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PLATE 3

PLATE 4

Figures 1, 2. *Indonautilus awadi* n. sp. Paratype MCZ 6101, from Middle Triassic *Beneckeia* beds, Makhtesh Ramon, Israel. X 1 .

Figures 3, 4. *Mojsvaroceras* n. sp. indet. MCZ 6099, from Middle Triassic *Ceratites* beds, probably higher part, at Makhtesh Ramon, Israel. X 1.

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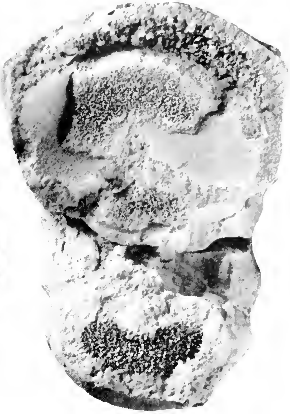

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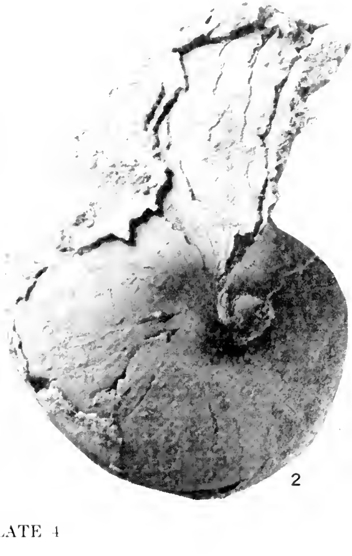

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PLATE 4

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

VOL. 123, NO. 8

BIRD SPECIATION ON THE AUSTRALIAN CONTINENT

BY ALLEN KEAST

Australian Museum

Sydney, Australia

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
MARCH, 1961

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY AT HARVARD COLLEGE

BULLETIN (octavo) 1863 — The current volume is Vol. 123.

BREVIORA (octavo) 1952 — No. 134 is current.

MEMOIRS (quarto) 1864–1938 — Publication was terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 3, no. 39 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 25 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1-3 are out of print; volumes 4 and 6 may be obtained from the Harvard University Press; volumes 5, 7 and 9 are sold by the Museum, and future volumes will be published under Museum auspices.

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No. 8 — *Bird Speciation on the Australian Continent*

By Allen Keast

Australian Museum, Sydney, Australia

CONTENTS

I. INTRODUCTION

This work is a study of vertebrate speciation on a continent. It seeks to understand the nature of the various forces operative in Australia, including the barriers breaking up distribution and leading to the isolation and divergence of populations. A quantitative approach is used to determine the number of new species currently evolving and the "potential" of the continent for producing further species.

Our basic knowledge of the speciation process has been derived from the study of the faunas of archipelagos and the many striking illustrations to be found there provide the classic examples. Continents, lacking the more bizarre intermediate forms and obvious distributional barriers (e.g. areas of sea), present a much less convincing case for geographic speciation. Thus, notwithstanding various fine studies, one school (Goldschmidt, 1940, p. 183) categorically denies that the infraspecific variation that is such a feature of continental populations can be an intermediate step in the formation of new species. Such variation, it is maintained, is "dead end" and of a purely local adaptive nature. A large number of clear-cut examples of continental speciation and the circumstances surrounding them are detailed here and explained. In order, moreover, to arrive at a quantitative comparison of the potential of archipelago and continent for giving rise to new species, the number of morphologically differentiated, isolated forms in Australia and an archipelago area of equivalent size are calculated.

It is now generally accepted that the successive steps leading to the completion of speciation are as follows:

(a) Part of an individually variable population becomes spatially isolated from the parental stock.

(b) Under conditions of isolation it diverges genetically, ecologically, physiologically, and morphologically.

(c) The differences become increasingly great.

(d) Finally, the isolates become so different from each other that they can no longer successfully interbreed, i.e. they are reproductively isolated. The ultimate proof of this, of course, is only forthcoming in those cases when, under natural conditions, the two forms secondarily come together and do not interbreed.

Mayr (1950a) has listed some of the proofs for geographical speciation as follows: (a) the occurrence of geographic variation in species characters; (b) the existence of borderline cases between subspecies and species; and (c) "circular overlaps," that is, cases where the end members of a chain of interfertile races meet and do not interbreed. Recently completed speciation is indicated by examples of: (a) double invasions, (b) superspecies, (c) marginal overlaps of closely similar species without interbreeding. Of particular significance also is the occurrence of allopatric hybridization, the result of a premature reuniting of differentiating isolates (i.e. before specific distinctness has been reached).

The approach in the present instance is to investigate the occurrence of intermediate stages in the speciation process and their frequency, and to seek and detail cases of the important associated phenomena. Each species has been studied to determine if it is monotypic or if geographic variation (clinal or in association with isolation) occurs. Isolates are graded according to the degree of their differentiation, and the total number for each species, family, and ecological subdivision calculated. The significance of various aspects of species ecology on variation and speciation, in particular the vegetation formation (habitat) occupied and nature of seasonal movements, is treated in detail.

Four hundred and twenty-five of the 531 breeding land and freshwater bird species and semi-species occurring in Australia (80 per cent of the total) are included in the present study.

II. MATERIALS AND METHODS

The present work was initiated in the period 1953-1955, when the writer was a Fulbright scholar at Harvard University. The basic material is from two sources: (a) systematic studies by the author (245 species) and, (b) recent taxonomic reviews, i.e. by workers using the ''new systematics'' (180 species). The bulk of the writer's work was carried out on the bird collections of the American Museum of Natural History, New York, which are easily the world's most comprehensive for the Australian and Pacific regions. They now include the Rothschild Collections and the bulk of the Mathews types, as well as much recent material from Queensland (J. Henry) and Western Australia (K. Buller). Other U.S. collections examined were the Gould Collection in the Philadelphia Academy of Sciences, the Arnhem Land Collection (H. G. Deignan) in the U.S. National Museum, and recent Queensland collections (by K. Stager) in the Los Angeles County Museum. Following the writer's return to Australia, material in the Australian Museum, Sydney (including recent collections made by the author in New South Wales, central and northern Australia), National Museum of Victoria, Melbourne, and South Australian Museum, Adelaide, was incorporated into the study.

In the studies of geographic variation, standard taxonomic methods have been used (see author's various papers), in all cases the emphasis being on the population, not the individual.

Published taxonomic data used in the work were obtained from the following sources: families Podicipitidae (Mayr 1943);

Accipitridae, Falconidae, and Pandionidae (Amadon, 1941; Condon, 1951a; Condon and Amadon, 1954); Ardeidae and Threskornithidae (Mayr, 1943; 1945b; and Amadon, 1942; Amadon and Woolfenden, 1952); Anatidae (Mayr and Camras, 1938; Mayr, 1940a, 1945b; Amadon, 1943; Amadon and Woolfenden, 1952; Ripley, 1942); Rallidae (Peters, 1934; Mayr, 1949); Psittacidae (Condon, 1941; Mayr, 1951; Cain, 1955); Sittidae (McGill, 1948; Mayr, 1950b); Cracticidae (Amadon, 1951); Grallinidae (Amadon, 1950a); Ptilonorhynchidae (Mayr and Jennings, 1952); and the following genera: *Geopelia* and *Lophophaps* (Mayr, 1951) in the Columbidae; *Acrocephalus* (Mayr, 1948) in the Silviidae; *Pachycephala* (Mayr, 1954a); *Falcunculus* and *Oreoica* (Mayr, 1953a, b); *Orthonyx* (Mack, 1934a); *Gerygone* (Meise, 1931); *Malurus* (Mack, 1934b; Serventy, 1951); *Sericornis* (Mayr, 1937; Mayr and Wolk, 1953); *Acanthiza* (Mack, 1936; Mayr and Serventy, 1938) in the Muscicapidae; and *Zosterops lutea* (Mees, 1957) in the Zosteropidae.

In addition, the general study by Condon (1951b) on the birds of South Australia contains much basic taxonomic information.

Detailed studies of geographic variation were carried out by the author on the following: the families Turnicidae, Pedionomidae, Columbidae, Alcedinidae, Menuridae, Atrichornithidae, Campephagidae, Artamidae, Meliphagidae, Zosteropidae, Dicaeidae, Oriolidae, the subfamilies Estrildinae (Ploceidae) and Muscicapinae (Muscicapidae); and the genera *Megalurus* (Silviidae), *Climacteris* (Sittidae), *Orthonyx, Sphenostoma, Drymodes, Psophodes* (Cinclosomatini, Muscicapidae), and *Epthianura, Ashbyia, Smicrornis, Aphelocephala, Hylacola, Calamanthus, Cthonicola, Origma, Pycnoptilus, Cinclorhamphus, Amytornis, Dasyornis,* and *Stipiturus* (Malurini, Muscicapidae). The majority of these studies have now appeared, or will later appear, as separate papers. Those so far published are: Oriolidae and *Megalurus* (Keast 1956a, b); *Aphelocephala, Dasyornis, Stipiturus,* Alcedinidae, *Climacteris* (Keast 1957a-e); Muscicapinae, *Amytornis, Epthianura* and *Ashbyia, Dicaeum,* Artamidae, Estrildinae, *Psophodes, Smicrornis,* Campephagidae (Keast 1958a-i).

A marked advantage of using birds for studies in speciation is that there is a great amount of data on distribution, habitat and general ecology available in the literature. This applies equally well in Australia. Included in the standard works consulted in the present study are: North, 4 vols. (1901-1914), Mathews, 12 vols. (1910-1927), Serventy and Whittell (1951), Mayr (1941, 1944a, 1945a), and the periodicals, *The Emu*, and *South Australian Ornithologist*, now in their 58th and 44th year of publication, respectively. Field workers in various parts of Australia have kindly made supplementary material available. In addition, the writer has had the advantage of having worked on the birds of eastern Australia over a number of years and to have made field trips as follows: central Queensland (1950, 1951), Bass Strait islands (1951), Kimberleys, coastal Northern Territory, and north Queensland (1952), Victoria (1951, 1955), central Australia (1952, 1958), southeastern South Australia (1958), western New South Wales, including the mallee regions (1956-1959), southwestern Australia and the Barlee Range (midwestern Australia) (1959). Besides acquiring taxonomic material, this has made it possible to check distributional limits, degree of attachment to habitat, aspects of seasonal movements, and to look at certain contact and hybrid zones.

Information on the Australian continent as an environment has been drawn from various official and other sources. In the case of the map showing former connections between Australia, New Guinea, and Tasmania, the 150 and 300 ft. isobaths are calculated from the sea depths shown on the Australian sheet of *Carte Generale Bathymetrique des Oceans*, 3rd Edition, 1942, Monaco. The map showing the limits of the Australian and Asian continent shelves is adopted from that in Mayr (1945c). Physiographic data are primarily from the 1942 Orographical Map of Australia by H. N. Warren, and Hills (1949). Data on temperature, rainfall, and associated factors, are from various official maps (undated), the Climatological Atlas issued by the Commonwealth Meteorologist (also undated), Leeper (1949), and the recently published Atlas of Australian Resources, Department of National Development, 1951-1955. The climatic map is based on the chart of Dr. J. Gentilli (undated). Other climatic maps, more precise and detailed, are to be found in Andrewartha and Birch (1954) and in the Atlas of Australian Resources, cited above. The maps of vegetation formations and soils are simplifications of those of Prescott (1931) and Wood (1949). Information as to Pleistocene and post-Pleistocene climates and vegetation changes is from Browne (1945), Crocker and Wood (1947), Gentilli (1949), David (1950), Fairbridge (1953), Crocker (1959a), and Wood (1959).

III. DEFINITIONS AND TERMINOLOGY

For the purposes of the present study it has been necessary to depart somewhat from the terminology normally used by taxonomists. This applies particularly to the dropping of the term "subspecies" or "race" which, as used, simply means a morphologically differentiated population and tells nothing of evolutionary potential. The emphasis here is on isolation and hence the term "isolate" is used. Where subspecies names come into the text, it is as a ready means of referring to a form that already bears a name in the literature.

Species: The modern biological definition for the species is followed, the criterion being reproductive isolation. Care is taken to draw attention to, and view somewhat differently, those species that are members of superspecies (i.e. that are allopatric representatives), and that fall into the category of "semi-species" (see Mayr, 1942). The latter are the distinctive isolates of uncertain genetic status that the taxonomist may call species because they have reached a significant stage of morphological differentiation and for the sake of expediency.

Isolate: This is a population or populations isolated from the main stock by a geographic barrier so that interbreeding is prevented. Isolates may be undifferentiated, slightly differentiated, moderately or well differentiated, the last-named being forms in which speciation is well advanced.

In calculations of the number of morphologically differentiated isolates one stock is set aside as the "parent" from which the isolates are diverging. For the sake of consistency, in comparisons between continent and archipelago, in those species that range through both, one form in each is set aside as "parental."

Species that do not vary geographically, or have only clinal variation, do not, of course, have isolates.

Population: This is used as an inexact term to mean simply the members of a species inhabiting a restricted area. It is credited with the morphological characteristics of a *series* of adult specimens from that area.

Morphological characters: Those used are variation in colouration and colour-pattern, the dimensions of the appendages (wing length [a good criterion of over-all size in birds], bill length, tail length) and, sometimes, the ratios of the length of one appendage relative to another. The term "morphological" is used to stress the fact that it is the variation visible in the preserved specimen that is being considered.

Hybrid zones: These are characterized by the presence of very variable populations, with extreme types, as well as a range of genetic recombinants being present. Most are narrow but in some cases a rather broad zone of intergradation occurs.

Hybrid zones mark the breakdown of a former barrier and the reunion of isolates that had reached a marked degree of morphological differentiation. A minor amelioration of climate in Australia, and in some cases human interference with habitat, is enabling various species to extend their range at the present time. Only a minority of them, however, have as yet contacted their geographic counterparts to form hybrid zones or zones of overlap.

Stepped clines: The presence of a "step" in a cline is evidence of former isolation and there are good examples of this phenomenon in a few Australian bird species, e.g. *Pachycephala pectoralis* (Mayr, 1954a). Minor zones of intergradation that may not, or do not, indicate secondary junction (note also the remarks of Miller, 1955) are discussed separately.

Continuous clines, though they may involve peripherally adapted forms that could diverge rapidly if isolated, do not form a stage in the speciation process. Hence they receive only passing attention.

Barrier: This is an area within, or at the edge of, the range of a species where it cannot thrive because of its innate ecological limitations. The term is used here strictly as a geographic or spatial concept.

The well defined distributional barriers, especially those that have given rise to distinctive isolates, are the critical ones here.

Habitat: This term is used in a broad sense to mean the basic vegetation formation occupied by a species.

About ten vegetation formations are of major importance to Australian birds: rain forest (under which may be included monsoon or pseudo-rain forest), sclerophyll forest, savannah woodland, savannah grassland, mulga, mallee, desert (spinifex) grassland, gibber desert, mangroves, and swamps and rivers. The majority of bird species occur in only one, or are common in only one, of these formations, sometimes being restricted to a specialized sector, association or sub-association within it (e.g. plateau-top heathland within the eastern sclerophyll sector). Habitat specificity is discussed in Section VI.

The significance of the vegetation formation in bird distribution and speciation lies, of course, in the fact that it represents a zone of relative physical and biological constancy. It is to these grouped factors that species have adapted and specialised during their development. "Habitat" is as valid a species character as morphological or genetic criteria, in most cases.

Refuge: This term refers to fertile or semi-fertile areas, mostly mountainous or hilly sections, in which plants and animals have been able to persist during arid periods.

Australia is currently in an arid phase, with marked aridity stemming from the early Recent. The rain forest, sclerophyll forest, and savannah woodland areas of the continent are today broken up into a disconnected series of peripheral segments, some of vast extent. Use of the term "refuge area" should not carry the inference that species "retreated" into them with the onset of aridity, but that only the stocks inhabiting those areas were able to survive.

Sedentary or resident species: This refers to a species the members of which do not undertake seasonal movements but, as adults at any rate, spend the year in the general vicinity of their breeding territories. There is a minimum intermixture of individuals from the different parts of the species range in this group.

Migratory species: This term is used for species that have a south-north migration and regular breeding areas. They are typically inhabitants of the better watered coastal forests where conditions are uniformly good. Examples: *Coracina novaehollandiae* (eastern Australia) and *Artamus cyanopterus.*

Nomadic species: This term denotes those species that: (a) undertake extensive group movements of irregular amplitude and direction and, (b) breed wherever conditions happen to be suitable, e.g. *Epthianura tricolor* and *Histriophaps histrionica.* (See also Section VI).

Nomenclature: That of Mayr and Amadon (1951) is followed in the present work. The species order is that of the 1926 Checklist of the Royal Australian Ornithologists Union.

IV. THE AUSTRALIAN CONTINENT AS A BIOTIC ENVIRONMENT.

The Australian continent has a land area of 2,984,000 square miles, about three-quarters of that of Europe (including European Russia). It is approximately the same size as the United States and is some twenty-five times the land area of the British Isles. It has been a stable land mass for a considerable portion of its geological history and Archaean rocks outcrop over an extensive area.

Australia differs from the other continents in various ways including:

(a) Spatial isolation from other large land masses (Figs. 1, 2).

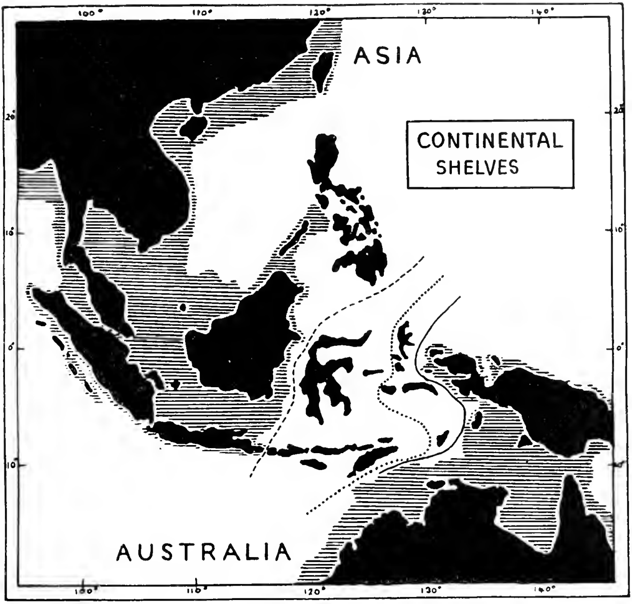

Fig. 1. Australia in relation to Asia, and showing limits of continental shelves (100 fathoms or 600 foot line). The dashes indicate Wallace's Line (original), the dots Weber's Line, and the continuous line the western limits of the Australo-Papuan continental fauna.

At the height of Pleistocene glaciation the sea level only fell 300 feet. The cross-hatched areas nevertheless correspond fairly well with the extent of land at that time. (Figure modified from that in Mayr, 1945e).

(b) General flatness, mountain barriers to dispersal being virtually nonexistent (Fig. 3).

(c) Absence of areas of extreme cold, the winter snowbelt amounting to only a few hundred square miles. There are no permanent glaciers or snowfields. The over-all climate varies from subtropical to cold temperate. The mean annual temperatures range from over 80°F. in the tropical north down to 45°F. in the highlands of the south. Daily minimum temperatures for July (coldest month) are 60-70° and 30-45°F. respectively, and daily maximum temperatures for January (hottest month) are 85-90° and 60-65°F., respectively.

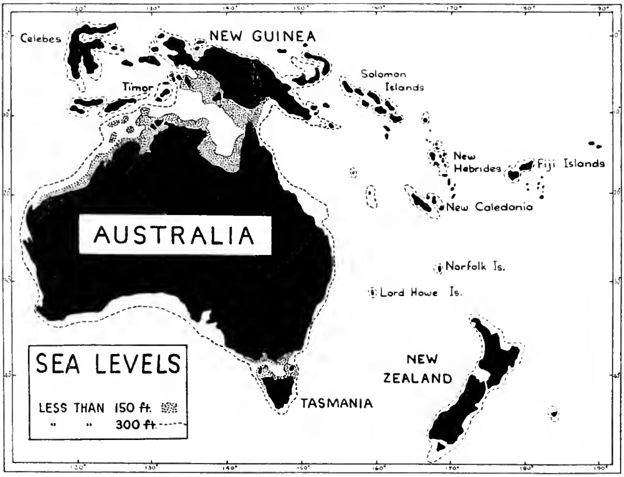

Fig. 2. Australia in relation to the islands to the north and east. The stippled areas indicate the land extensions that would follow a 150 foot drop in sea level, and the dashes show the 300 foot line. Tasmania and New Guinea were twice connected with Australia during the Pleistocene when the sea level fell 300 feet.

Deep water isolates Timor, New Zealand, and the islands to the east and separates New Britain from New Guinea.

(d) Generalized aridity. Agriculturists classify Australia as being only one-third fertile, with the remaining thirds semi-arid and arid, respectively. Rainfall (Fig. 4) is the all-important factor governing the distribution of life in Australia.

(e) The arrangement of the basic vegetation formations (which form the bird habitats) into broad parallel, north-south (mostly), or east-west zones (Fig. 5). The altitudinal zonation of plants and birds that is such a feature of the Rockies and other high mountain regions of the world is virtually absent in flat Australia.

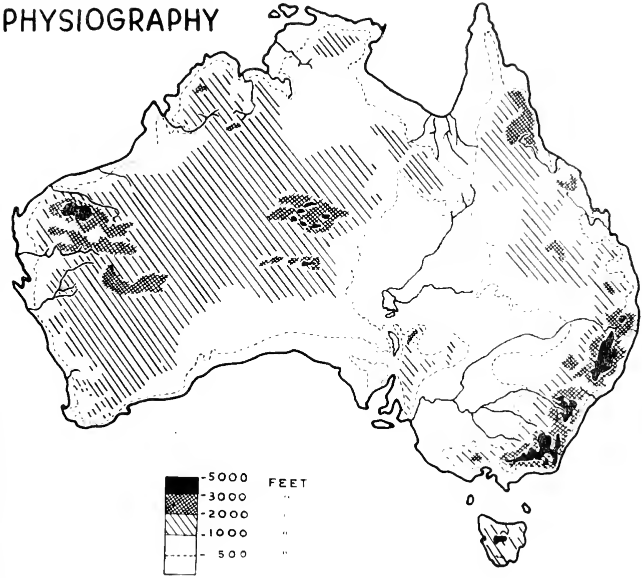

Fig. 3. Physiographic map of Australia. The continent is relatively flat. Mountains are not, per se, significant barriers to avian distribution. Their control of distribution, by way of rainfall and vegetation, however, is profound.

The dotted line indicates drainage patterns. (Map redrawn from that of Hills, 1949).

Physiography, Climate and Vegetation

Physiography: The continent falls into three physical subdivisions (Fig. 3): the Great Plateau or Archaean Shield that covers the western half of the continent, the Central Basin, and the Eastern Highlands (Hills, 1949; David, 1950). The backbone of the last-named is the Great Divide, the range that extends southwards down the full length of the east coast, thence to Tasmania and westwards to central Victoria. It is by far the most significant physiographic feature on the Australian continent and not only influences climate and vegetation over a wide area but permits a richness and diversity in the flora and fauna that would otherwise be impossible. Nevertheless, only relatively

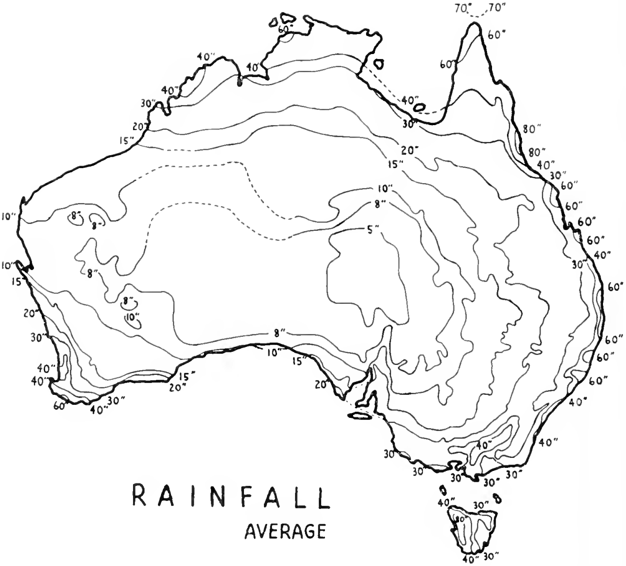

Fig. 4. Rainfall of Australia (average annual figure in inches). The pattern is one of concentric zones of increasing rainfall outwards from an arid central area. The desert extends to the coast in the south and west. The eastern, southeastern, southwestern sections, and a small area in the north, are fertile.

(Map adapted and simplified from that in the Atlas of Australian resources — Rainfall; Published by the Department of National Development, 1952.)

restricted parts of it exceed 4000 feet in height and the highest peak in Australia, Mount Kosciusko in the southeastern section, is a mere 7,300 feet in height.

Here and there over the surface of the continent, elevated areas, residual masses, and dissected plateaux take the form of mountain ranges. Amongst the most interesting of these from the faunistic viewpoint are the Mount Lofty and Flinders Ranges in South Australia, the Macdonnells and other ranges in central Australia, the Darling Scarp and Stirling Ranges in the southwest, Hamersley Ranges and the Kimberley district in the northwest of the continent (Fig. 3). Though typically these do not rise more than a couple of thousand feet above the surrounding plain they have a marked local influence on rainfall and vegetation and

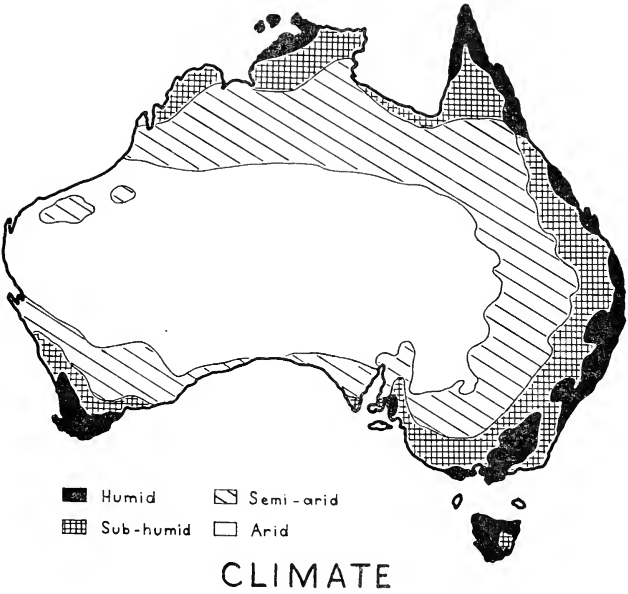

Fig. 4a. A simplified climatic map of Australia. Derived by J. Gentilli (Thornthwaite formula).

permit the existence of various forms of life that would otherwise be impossible.

Rainfall: The rainfall patterns of Australia will be seen from the map of average rainfall (Fig. 4). The isohyets take the form of concentric zones of increasing rainfall extending outwards from an arid interior. The transition is particularly well defined in the east where the belts extend from north to south parallel with the coast. In places, tongues of dry country extend through from the interior to the coast, breaking up the more fertile country into sectors.

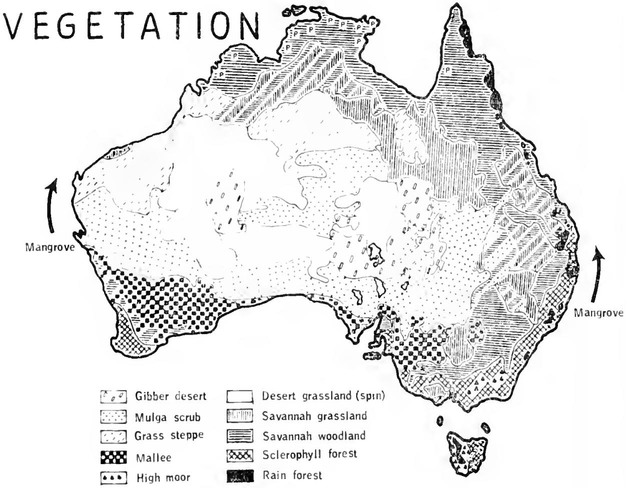

Fig. 5. Major vegetation formations of Australia, simplified from Prescott (1944) and Wood (1949). For explanatory notes see Table 1. There is a close relationship between the distribution of bird species and that of the major vegetation formations, with gaps in the formations acting as isolating barriers. *M* = mangroves; *P* = pseudo-rainforest (riverside).

Two main systems operate to produce the Australian rainfall, a winter one that moves up over the southern part of the continent (the "Antarctic System") and a summer one (the "Tropical System") that brings monsoonal rains to the north of the continent. The north of the continent has a wet summer and a dry winter, whilst in the south the reverse is the case. Since, however, the summer is hot in the north the rainfall there is less effective and the over-all climate is dry. The Eastern Highlands ensure that the east and southeast of the continent benefit both from the summer and winter systems and have a comparatively even rainfall. The central regions of the continent are towards the limits of penetration of both systems, either or both of which may fail. The 10-inch line in the south and 15-inch zone in the north outline the limits of the desert.

Other facets of rainfall in Australia are its unreliability over large sections and the high rate of evaporation, factors greatly influencing plant growth. The irregularity of the rainfall in the interior explains the high proportion of nomads in the avifauna there.

The climatic zones in Australia (Fig. 4a) reflect the rainfall picture.

Vegetation: The basic vegetation zones occurring on the Australian continent and a summary of their characteristics, are set out in Table 1. The approximate area of the continent covered by each (author's calculations) is given in Table 2. The close link between rainfall and the distribution of the basic vegetation formations in Australia will be seen from a comparison of Figures 4 and 5.

Rain forest is restricted to the eastern seaboard and is broken up into pockets. Sclerophyll forest, eastern and southern in distribution is also largely restricted to the coastal regions and is discontinuous.

Savannah woodlands occur as broad tracts across the north and down the east of the continent (mainly).

Savannah grasslands, mulga, and spinifex desert (desert grassland) are the semi-arid to arid country formations. They occur as broad and continuous zones with the latter two occupying the central areas.

Mallee, a stunted but floristically diverse formation, occurs in broad southeastern and western tracts (with some discontinuity) in the dry southern inland of the continent.

Mangroves extend practically right around the Australian continent but the rich and diverse tracts that support specialized mangrove bird species are restricted to the northernmost two-thirds. The swamps and marshes (not shown because of their relatively small extent) and rivers (homes of the water-birds) are developed to by far the greatest extent in the better watered southeast of the continent (Victoria and New South Wales). Even so, a good proportion of them are temporary.

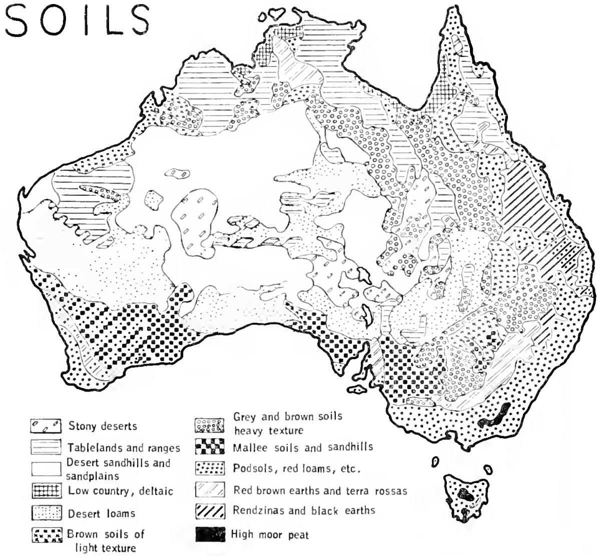

Fig. 6. The soils of Australia. Map is a simplified version of that of Prescott (1944), reproduced by Taylor (1949). Definitions of soil types are given by R. Crocker (see Keast, 1959a).

Physiography, rainfall, and soils, control the distribution of vegetation.

Soils: The major soil types occurring in Australia will be seen in Figure 6. The characteristics of these have been summarized by Crocker (*in* Keast, 1959a). Attention to the fact that the zonal soil groups in Australia follow a pattern somewhat similar to rainfall has been directed by Wood (1959). Again, there is a broad, but not absolute, zonal sequence and correspondence between soil type and vegetation.

Soil history in Australia, and its influence on bird distribution, through the vegetation, will be discussed in Section XI.

Spatial Relationship of Australia to other Land Masses

The distance between Australia and the nearest point of the Asiatic mainland today exceeds 2000 miles. This isolation dates back to the beginning of the Tertiary, a period of some 50,000,000 years.

The limits of the Australian and Asian continental shelves (100 fathom or 600 foot line) will be seen on Figure 1. The former, it will be noted, extends out for only a short distance but the latter includes Borneo and Java, over one-third of the distance towards Australia. During the Pleistocene emergence the sea-level is believed to have twice fallen some 250-300 feet, and it is obvious that the Asian continent must have extended a considerable distance towards Australia. Nonetheless, the faunistic differences between the two continents have been preserved. This underlies the significance of the intermediate deep-water gap, the islands within which have been highly unstable geologically. These islands, moreover, are "ecologically impoverished" and apparently only capable of supporting a somewhat limited number of bird species. On these grounds also they represent a "distributional bottleneck." A discussion of Wallace's Line is beyond the scope of the present paper. Several recent authors have, however, reviewed its zoogeographic significance; these include Scrivenor et al. (1943), Mayr (1945c), and Darlington (1957).

The islands adjacent to the Australian continent and their history are as follows:

Timor: This lies some 350 miles to the northwest of Australia, a gap that was narrowed to perhaps 50-70 miles at the height of the Pleistocene emergence. As will be seen from Figure 1, however, there is a narrow tract of deep water immediately to the east of Timor. The avifauna of Timor is a blend of species of western and eastern origin (Mayr, 1944a).

New Guinea: This large island is only 100 miles from Australia at its closest point. The intermediate water is shallow, extending down to only about 30 feet in the section to the north of Cape York. New Guinea has repeatedly been in direct contact with Australia. This was the case during part of the Tertiary and on two separate occasions in the Pleistocene.

New Caledonia: This island, 750 miles to the northeast of Australia, is separated by deep water and its isolation is of long standing.

New Zealand and Lord Howe Island: These islands lie, respectively, 1200 and 350 miles to the east of Australia. Both are regarded by geologists as "continental remnants," though a submarine trough extending down to 12,000 feet isolates New Zealand today. The nature of any pre-Tertiary connections with Australia are, however, highly speculative.

Tasmania: This island lies about 140 miles off southeastern Australia but with islands half-way across, and has a purely Australian fauna. Intermediate ocean depths only extend down to perhaps 150 feet and, like New Guinea, Tasmania was directly connected to Australia during part of the Tertiary and Pleistocene.

The influence of the surrounding land masses on the Australian avifauna has obviously been relatively slight, a fact that makes the continent ideal for speciation studies. Not only is the continent surrounded by areas of deep sea but, if Tasmania be included with Australia, only to the north has there been "interference" from outside. New Guinea has, however, continuously contributed new bird species to Australia.

V. THE AUSTRALIAN AVIFAUNA

Australia is credited with 707 species of birds by the Official Checklist of the Royal Australasian Ornithologists Union (1926). The recent treatment of Mayr and Serventy (1944), however, rightly reduces the number to some 651 species. There are 37 species of breeding seabirds, 83 visitors, 531 land and freshwater birds (29 of which come into the category of semi-species), with 14 being restricted to adjacent islands. It is on this total of 531 species that the calculations in the present work are based.

In accord with its being the smallest land mass, Australia has less bird species than the other continents, as the following figures of Stresemann (1927-1934) will show:

Australia	531 species
Africa	1,750
South America	2,500
North America	750
Palearctic region (Europe and Asia)	1,100

The tropical island of New Guinea, immediately to the north of Australia, with only one-tenth of the land area, but dominated by tropical rain forest and high mountains, has no fewer than 509 species of land and freshwater birds, together with 28 semi-species, and 29 inhabiting adjacent islands, a total of 566 species. Thus it has a richer avifauna than Australia. If the 191 species common to both be eliminated, the combined total for Australia and New Guinea is 906, a sum that brings the section more into line with the major land masses of the Northern Hemisphere.

The Australo-Papuan region is one of the major zoogeographic subdivisions of the world and, in conformity with its peculiar mammalian, amphibian, and freshwater fish fauna, is rich in endemic bird families, subfamilies, and genera. In contrast with some lower vertebrate groups (freshwater tortoises, hylid frogs), various invertebrates and some plants, and despite the occurrence of flightless ratites, numerous parrots, etc., on both, Australia has no close affinities with the avifauna of South America. Likewise, supposed direct relationships with certain African elements (e.g., between *Promerops* and the Australian Meliphagidae) are now open to question (Mayr and Amadon, 1951). Many bird families do, however, extend from Asia to Australia, and some from Africa or Europe, through Asia, to Australia. Such may be equally well developed in both regions, e.g., Turnicidae, Campephagidae, Ploceidae, Zosteropidae. More commonly, however, only one or two species of such Palaearctic or Oriental families extend to, or occur in, Australia: Meropidae, Pittidae, Timaliinae, Sylviinae, Motacillidae, Nectariniidae, Coraciidae, Sturnidae, Oriolidae, Dicruridae. Avifaunal interchange across Wallace's Line and down the ''impoverished'' Indonesian island archipelago has been discussed by Mayr (1945c), Darlington (1957), and others.

The families and subfamilies endemic to the Australo-Papuan region have been listed by Darlington (1957) and Keast (1959b). Those occurring in Australia proper, and the number of species comprising each family, are as follows: Casuariidae (cassowaries), 1; Dromaeidae (emus), 1; Megapodiidae (incubator-birds), 3; Pedionominae (collared hemipodes), 1; Loriinae (honey lories), 6; Kakatoeinae (cockatoos), 10; Menuridae (lyrebirds), 2; Atrichornithidae (scrub-birds), 2; Malurinae (Australian warblers), 64; Meliphagidae (honeyeaters), 65; Cracticidae (Australian butcher-birds), 14; Grallinidae (mud-nest builders), 3; Ptilonorhynchidae (bower-birds), 8; Paradisaeidae, (birds of paradise), 3. Two hundred and thirteen species of Australian land and freshwater birds, or 35 per cent of the total, belong to these endemic groups. If, however, Australia and New Guinea be grouped together, with their total of 906 different species, the number of species belonging to these groups is found to reach 369 (41 per cent).

In addition to endemic families and subfamilies Australia has various endemic genera belonging to cosmopolitan families such as the Anatidae (ducks), Columbidae (pigeons), and Ploceidae (finches). The Strigidae (owls), Cuculidae (cuckoos), Rallidae (rails), and others are each represented by various endemic species. In contrast to this, interestingly enough, a couple of cosmopolitan bird species extend to Australia, e.g., the owl *Tyto alba*, the falcon *Falco peregrinus*, and the grebe *Podiceps cristatus*.

Considerable radiation has occurred in the Australo-Papuan region in various cosmopolitan families. Thus, Australia now has 18 species of ducks and geese, 23 pigeons and doves, 51 parrots (though a proportion of these are lories and cockatoos), 10 kingfishers, and 12 cuckoos.

From the viewpoint of its origin, the Australian avifauna could be said to have been built up by a series of waves of colonization from the north over a prolonged period, or by successive colonizations superimposed upon the earliest elements. Isolation has been fairly complete throughout.

VI. THE SAMPLING OF THE AUSTRALIAN AVIFAUNA

Eighty per cent (425 out of 531 species) of breeding land and freshwater birds are covered.

The sampling of species in the present work, has been a random one. Only a couple of families of lesser importance are unrepresented. The proportion of species of New Guinea-Pacific and Australian origin in the sample approximates to that actually occurring, as does the proportion of species with the different kinds of distribution in Australia, e.g., southern as against northern, peripheral and inland, extensive and restricted. The ratio of species inhabiting the various basic vegetation formations and of those falling into the various categories of seasonal movement is likewise maintained in the sample.

In the following, stress is placed on the relationship between speciation and (a) the phylogenetic group (i.e. family) to which a species belongs, (b) the vegetation formation it occupies, (c) the nature of its seasonal movements.

Sampling According to Classification and Family Categories

The classification and subdivisions of the Australian land and freshwater bird fauna are set out in Table 4. The number of species in each family and sample used in the present study are shown in the first column. Thirty-one families are covered in toto whilst some 90 per cent of the Muscicapidae and more than half the parrot species are included. The only important families unrepresented are the Strigidae (8 species), and Cuculidae (11 species).

Sampling According to Habitat (Vegetation Formation) Occupied

The major vegetation formations occurring in Australia, and the approximate continental area covered by each plus its percentage of the whole, are set out in Table 2. In succeeding columns the number of bird species restricted to or reaching its greatest abundance in each formation are shown, together with its percentage of the total avifauna. The final column represents a calculation of the number of square miles of habitat per species, to give a figure for the relative richness of each vegetation formation.

The sample of each type used as the basis for all the calculations in this work is set out in the first column of Table 5.

Savannah woodland, savannah grassland, mulga, and spinifex desert, cover the largest areas of the continent. By contrast, rain forest and mangroves, though covering only a small area, are richest, on the one hand, in terms of number of bird species and, on the other, in number of species per square mile of habitat. The largest number of species, however, could be said to be specialized for life in sclerophyll forest and savannah woodland. This figure, it should be noted, does not represent the number of bird species that could be seen in a day's observation in a typical area of each habitat, for in a savannah woodland, particularly, there is a relatively greater geographic replacement of species as between the north (tropical savannah) and the south. Rather, it expresses the number of species that are, basically, inhabitants of each.

In the compiling of Table 2, it was apparent that the avifauna of the more specialized vegetation formations, the rain forest, sclerophyll forest, mallee, desert (spinifex) grassland, mangroves, and swamps and rivers, tended to be fairly specific and conservative in habitat choice. Hence, little difficulty was had in allocating species to a category. This did not apply, however, to the more "transitional" types of vegetation formation: savannah woodland, savannah grassland, and mulga, which not only have much in common but interdigitate and overlap extensively. The dominant species in savannah grassland (or savannah woodland) may also be common in savannah woodland (or vice-versa) and

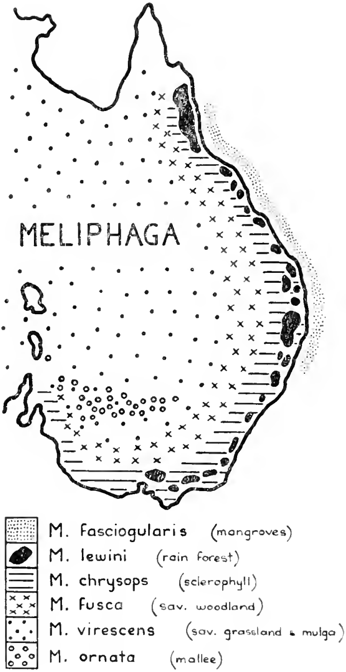

Fig. 7. Distribution of 6 species of the genus *Meliphaga* (honeyeaters) in eastern Australia to show correlation with major vegetation formations. The map is somewhat diagrammatic. Six species are inhabitants respectively of mangroves, rain forest, sclerophyll forest, savannah woodland, savannah grassland — mulga, and mallee.

This is an exceptionally good example of a phenomenon seen to at least some extent in most bird genera.

mulga, and penetrate the dryer sclerophyll forests and mallee. In these cases the alternative remained of creating several additional "habitat categories" or placing the species under the vegetation formation in which they were especially prominent. For the sake of simplification the latter course was chosen. The figures for savannah woodland and savannah grassland are placed in brackets in Table 2; they are probably relatively too high.

Apart from the above, a number of species occupy a life zone that is a continuum between two or more formations, e.g. the "leafy canopy," mistletoe. Again, large hawks, crows, small aerial feeding species (e.g. swallows), and a few others, are little influenced by vegetation in their distribution. They have a range that is virtually continent-wide. For the sake of completeness these are included in whichever of the "intermediate-type" habitat categories they are especially prominent.

Each bird species is included only once in the calculations.

The whole problem of allocating species to habitat categories is much simplified in Australia, fortunately, by the basic vegetation formations being arranged in broad, parallel, zones.

Sampling According to Seasonal Movements

The seasonal movements undertaken by Australian land and freshwater bird species are complicated and every stage in the transition from one to another of the extremes is present. Thus, amongst the south-north migrants are species in which the movement is restricted to the more southern populations, or to a proportion of the individuals of these populations. In others the movement is entire. Amongst the nomadic species are some that are sedentary for a year or more, moving with the onset of a drought, and others that are nomadic in part of the range only. In the more typical nomads, however, the movements are general, irregular, occur frequently, and are of considerable amplitude. Many have, seasonally, a south-north bias to the movements.

For the purposes of the present work, species are broadly grouped into the three categories according to the nature of the seasonal movements over the bulk of the species range.

Grouped in this way, the Australian land and freshwater birds are as follows:

TABLE 7

	In Fauna		*In Sample*	
	No. of Species	% of Whole	No. of Species	% of Whole
Sedentary species	351	66	294	69
South-north migrants	42	8	32	8
Nomadic species	138	26	99	23

The small number of true migrants and the relatively great importance of the nomadic way of life on the Australian continent, as compared to the Palearctic and Nearctic regions, will be noted. Nomadism is an adaptation to unreliable and uncertain rainfall, though, in Australia, a certain amount of this behaviour is associated with the blossoming of food trees. Migratory species, in the restricted south-north sense in which the term is used here, are, as noted, mainly inhabitants of the well-watered eastern section of the continent.

VII. VARIATION AND SPECIATION IN THE VARIOUS BIRD FAMILIES

Order PODICIPEDES

Family PODICIPITIDAE

(Grebes)

There are three grebe species in the Australian region, only one of which is endemic. All have an extensive Australian range, are nomadic, and are swamp and river forms, diving for submerged food.

Speciation

Where continental variation occurs it is of a clinal nature, vide *Podiceps novaehollandiae* (Mayr, 1943). Isolation and differentiation does, however, occur in this species beyond Australia.

Order FALCONES

Families ACCIPITRIDAE, FALCONIDAE, PANDIONIDAE

(Hawks and Eagles)

The Australian eagles and hawks number 24 species and constitute a most varied fauna. At the one extreme are small "hovering" kites and a kestrel, at the other the large eagle *Aquila* *audax* with wingspan of up to ten feet. The majority of the forms are endemics (4 genera, 15-16 of the species) that have diverged to a greater or lesser extent from counterparts in other areas of the world.

The various forms are specialized ecologically in various ways: as scavengers, rodent and insect feeders, hunters that catch birds in the air, and as fish-eaters. Many are nomads and their distribution depends on seasonal conditions and the whereabouts of prey.

All the Australian hawks are well differentiated species.

Speciation

Fifteen of the Australian Falcones either do not vary geographically, or have only insignificant clinal variation. This results largely from the mobility that goes with large size and the strongly developed nomadic tendencies of most species.

Of those that do vary geographically, one species *Falco berigora*, does so to a marked degree. It is improbable, however, that any of its forms are true isolates today (Condon, 1951a).

Distinctive southern and northern forms occur in four species with evidence in at least one (*Accipiter fasciatus*), and possibly others (*A. cirrhocephalus, Falco longipennis, Pandion haliaetus*), that this state of affairs has been built up by invasion of the continent from the north taking place in two waves. In *Accipiter fasciatus* these consecutive arrivals are now connected by a stepped cline (Condon and Amadon, 1954).

Aquila audax and possibly *Accipiter novaehollandiae*, show some evidence of interruption to gene flow across Bass Strait. The northwestern stock of *Aviceda subcristata* and the southwestern population of *Falco peregrinus*, each of which has differentiated to some extent, are apparently isolated.

Although there is evidence in a few species of minor isolation and range thinning, there would not appear to be any species being formed in the Australian hawks today. In the island section to the east of Wallace's Line, by contrast, the Australian species are broken up into about 43 morphologically differentiated isolates. This is exclusive of the variation occurring to the west of the Line in cosmopolitan, or Afro-Asian, species such as *Milvus migrans, Haliastur indus, Falco peregrinus,* and *Pandion haliaetus*.

Order GRESSORES
Families ARDEIDAE, THRESKIORNITHIDAE, CICONIIDAE
(Herons, Spoonbills, Ibises)

The 19 species that make up the Australian members of this order may be divided up as follows: — swamp bitterns, 2; mangrove bitterns, 1; egrets, 3; night herons, 1; stream and swamp herons, 4; reef herons, 1; estuarine herons, 1; spoonbills, 2; ibises, 3; storks, 1. All of these extend beyond Australia and a few belong to widespread superspecies. The majority of the forms are predominantly swamp feeders but the herons hunt in the open fields, fringes of streams, and tidal flats as well. One species is confined to mangroves and a second is exclusively a reef feeder.

The Australian Gressores almost all have a wide range on the continent and typically are nomads, moving around with seasonal conditions. Breeding areas vary somewhat from year to year, depending on water levels on individual marshes and streams (H. J. Frith, personal communication).

A couple of species, however, are seaside feeders, and exhibit little seasonal movement. These are the Mangrove Heron, *Butorides striata*, and the Reef Heron, *Demigretta sacra*.

Speciation

None of the members of this group vary geographically except (a) *Threskiornis molucca*, that apparently shows a slight south-north size cline, and (b) *Butorides striatus*, that has no fewer than five differentiated isolates (Mayr, 1943). Under circumstances of insular isolation in the southwest Pacific, by contrast, *Nycticorax caledonicus* has 2 distinctive isolates, *Dupetor flavicollis* at least 2, and *Butorides striatus* 4.

The Australian isolates of *B. striatus* occur as follows: (a) Shark Bay (unnamed form), (b) Ashburton River to Point Cloates (*rogersi*), (c) King Sound (*cinereus*), (d) Northern Territory and Melville Island (*stagnatilis*), (e) Cooktown area (*littleri*), and (f) New South Wales (*macrorhynchus*). These forms differ markedly in colour and size and one of them (*rogersi*) was long considered a distinct species. Mayr stresses the fact that the western and eastern groups are distinct, and suggests that they may have originated as a double invasion.

The pattern of isolation and differentiation in *B. striatus*, set out in Figure 8, is similar to that seen in some other mangrove birds (see Section IX).

Demigretta sacra has a similar distribution to *Butorides striatus* but does not vary geographically in Australia. It is a

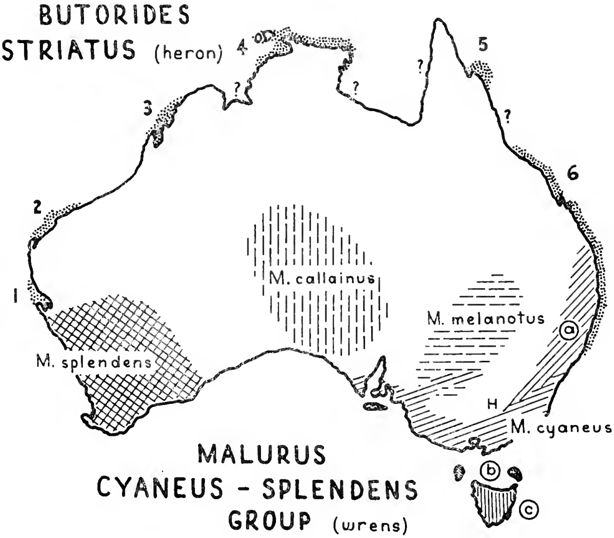

Fig. 8. *Upper:* Isolation and differentiation in the mangrove bittern (*Butorides striatus*). There is a chain of distinctive isolates along the western, northern, and eastern coasts (indicated by spotted areas and numbers). Range gaps correspond to areas where the appropriate habitat is apparently lacking.

Lower: Distribution of species and forms in the *Malurus cyaneus* — *melanotus* — *splendens* group of the blue wrens (see cross-hatched areas in lower half of map). The four major forms shown, though isolated from each other, are so distinct that (with the possible exception of *M. melanotus* and *M. callainus*) they must be regarded as (taxonomic) species. The habitats differ markedly, *M. cyaneus* inhabiting sclerophyll forest and thickets in savannah woodlands, *M. melanotus*, mallee, *M. callainus*, spinifex desert, and *M. splendens*, sclerophyll and dry scrubs.

M. cyaneus has isolated insular races on the Bass Strait islands and Tasmania. "H" refers to a minor zone of intergradation. The small letters, "a", "b", and "c" refer to races of *M. cyaneus*.

relatively "conservative" species, with only one morphologically differentiated isolate in the whole of the Pacific.

Order ANSERES
Family ANATIDAE
(Ducks)

There are 19 Australian species, many of them endemics. The fauna includes a number of curious monotypic genera such as the Black Swan (*Cheopis strata*), the Pied Goose (*Anseranas semipalmata*), the Cape Barren Goose (*Cereopsis novaehollandae*), the Pink-eared Duck (*Malacorhynchus membranaceus*), Freckled Duck (*Stictonetta naevosa*), and Musk Duck (*Biziura lobata*). By contrast, others are representatives of near cosmopolitan groups: teals, shovellers, and tree ducks.

The various members of the family are typically swamp and river forms, a few being animal feeders, but most are herbivorous or have a mixed diet. There are no true sea ducks in Australia.

Most species have a wide range. Some four are essentially southern, and three are confined to the tropical north. Only one species, *Cereopsis novaehollandiae*, has a really restricted range—the islands off the southern coast.

The most striking feature of the Australian Anatidae is the great mobility of most species. The Australian bird literature has many references to ducks arriving in various districts following heavy rain, remaining for a while and, with the drying up of the surface water, disappearing again. Recent banding work on one species, the teal *Anas gibberifrons*, has proven that individuals move seasonally between the north and south of the continent (e.g. Darwin — Perth, Darwin — southern New South Wales). The amplitude of movement of at least two other species (*Malacorhynchus membranaceus*, *Anas superciliosa*) is undoubtedly equally great.

The areas in which most duck species concentrate to breed vary somewhat from year to year but there is regular breeding both in southeast and southwest Australia (H. J. Frith, personal communication).

Speciation

The distinctive small teals, *Anas gibberifrons* and *A. castanea*, at one time considered to belong to the same species (Ripley, 1942) but now known to coexist over a wide area, represent the only case in which the circumstances of past speciation can be seen. The two apparently originated as a double invasion of the continent from the north, with *A. castanea* being the older inhabitant.

Geographic variation is negligible in the Australian Anatidae. In contrast with the situation on the continent, a number of Australian ducks show well marked differentiation in the island archipelagos to the north. Thus, *Dendrocygna arcuata* has at least one morphologically differentiated isolate, *Anas superciliosa*, one, and *Anas gibberifrons*, one.

Order GALLI
Family RALLIDAE
(Rails and Water-hens)

Of the 14 species occurring in Australia, three extend through from the Palaearctic region (*Porzana pusilla*, *Fulica atra*, *Porphyrio porphyrio*). A few others belong to cosmopolitan superspecies (e.g. *Gallinula tenebrosa*). Two species have a wide range through the Pacific (*Hypotaenidia philippensis*, *Poliolimnas cinereus*). Of the remainder, three species occur also in New Guinea and adjacent islands and/or New Zealand (*Rallus pectoralis*, *Rallina tricolor*, *Porzana tabuensis*, plus *Porphyrio porphyrio* mentioned above). Four species are restricted to Australia (*Eulabeornis castaneoventris*, *Porzana fluminea*, *Amaurornis ruficrissus*, *Tribonyx ventralis*), and one (*Tribonyx mortieri*) to Tasmania.

With the exception of the northern *Rallina tricolor*, inhabiting undergrowth and thickets near tropical streams, and *Eulabeornis castaneoventris* and *Poliolimnas cinereus*, living in mangroves (also in the north), the Australian Rallidae are swamp and marsh species.

Speciation

Nine of the Australian Rallidae either do not vary geographically or have only minor clinal variation. Of these, four have a relatively restricted range (north of the continent or on Tasmania only). The others are either highly nomadic (e.g. *Fulica atra*), or at least nomadic over part of the range (*Tribonyx ventralis*).

The most marked isolation and differentiation occurs in *Porphyrio porphyrio*, the southwestern form of which (*bellus*) is highly distinct, the Tasmanian isolate (*fletcherae*) somewhat less so. *P. porphyrio* is a sedentary species. The southwestern populations of *Porzana fluminea, Gallinula tenebrosa* and *Rallus philippensis* are apparently isolates, as are the Tasmanian populations of *Rallus pectoralis* and *Porzana tabuensis*. The distinctive endemic rail of Tasmania, *Tribonyx mortieri*, may represent an early isolate of *T. ventralis*-type stock, though a fossil rail from southern Queensland (*T. effluxus* Devis (1892); see Condon, 1954, p. 23) could indicate that it is derived from a heavier-bodied stock now extinct on the mainland. *Eulabeornis castaneoventris* has a morphologically differentiated isolate in the Aru Islands

In contrast with the minor amount of isolation and speciation within Australia, several of the rail species have a large number of distinctive isolates beyond the continent. *Rallus philippensis* has a total of 18 differentiating isolates in the section to the east of Wallace's Line (including New Zealand, New Caledonia, and Macquarie Island — Peters, 1934, p. 164), *Porphyrio porphyrio* about 8 (in New Zealand, the Chathams, Lord Howe Island, various Pacific islands), whilst *Porzana tabuensis* has them in New Zealand, New Caledonia, Fiji, and elsewhere. The capacity of the short-winged rails for colonizing oceanic islands is well known. Here they typically occupy grass thickets and undergrowth, not marshes.

Order GRUES

Family TURNICIDAE

(Bustard-quails)

The Turnicinae and Pedionominae, respectively, contain six and one species. One member of the former extends to New Guinea and beyond, and another to New Caledonia.

All are swift-running, swift-flying, ground-living birds, partly seed-eating but also taking insects, and requiring long grass and herbage for protection. The various species are specialized for life on the open plain, rocky hillsides, swampy ground, forests and dense scrub.

The various species of *Turnix* vary in bill form, some having slim, others heavy graminivorous-type, beaks. This situation is reflected in *Amytornis*.

Speciation

Only two forms show any speciation trends in Australia: the stationary *Turnix varia* and *Turnix castanota*. The former, inhabiting sclerophyll forest (and mallee), is a coastal form of the east and south. It has isolates, none of them very well differentiated, in Tasmania, the southwest corner of the continent, and on the Abrolhos Islands. *Turnix castanota*, a savannah woodland inhabitant of the northwest of the continent, has a distinctive isolate (approaching the extent of differentiation typical of a species) on Cape York (*olivei*).

The remaining species either do not vary geographically or show only clinal variation. Most, however, are either nomadic (e.g. *T. velox*), or else have only a restricted range (*T. melanogaster*, *Pedionomus torquatus*).

There could be a degree of isolation, past or continuing, between the northwestern and eastern forms of *Turnix pyrrhothorax*.

Order COLUMBAE

Family COLUMBIDAE

(Pigeons and Doves)

The Australian pigeon and dove fauna totals 22 species, two-thirds of them endemic. *Chalcophaps indica chrysochlora*, however, is the end member of a chain of forms extending through from India and thence east to the New Hebrides. *Geopelia striata* extends from Malaya to Australia. *Ptilinopus regina* and *P.* (*cincta*) *alligator* stem from the islands to the northwest of the continent (e.g. Timor) and the parental stock of the endemic eastern *Macropygia phasianella* apparently also entered the continent from that sector (Mayr, 1944b). *Ptilinopus superbus*, *Megaloprepia magnifica*, and *Ducula spilorrhoa* are fairly recent immigrants from New Guinea, whilst the parental stock of the endemic *Columba norfolciensis* must have also entered from the northeast.

Within the Australian continent today the pigeon-dove fauna falls into a large number of morphologically and ecologically distinctive types. The fruit pigeons are as highly coloured as the interior ground dwellers are plain.

The various species may be grouped ecologically as follows:—

(a) *Rain forest forms.* Arboreal fruit and berry eaters, 8 species.

Forest floor species, 2 species.

(b) *Ground feeding form of the coastal undergrowth* (southern), 1 species.

(c) *Small arboreal doves* which feed on the ground and have a northern or inland range, 3 species.

(d) *Pigeons of the interior grasslands and desert* 5 species.

(e) *Rock Pigeons*, requiring rocky outcrops, 2 or 3 species.

The eastern rain forests have a dense fauna, as has the plains country of the inland. The rock pigeons inhabiting areas of rocky outcrops, are interior and northwestern in distribution.

Only two species occur in the southwest corner of the continent and in Tasmania (*Phaps elegans* and *P. chalcoptera*).

Speciation

The circumstances of origin of most endemic genera and species cannot now be seen. Some speciation is, however, occurring today.

The large rain forest fruit pigeon, *Megaloprepia magnifica*, has morphologically differentiated isolates corresponding to each of the three main tracts of rain forest: northern New South Wales-southern Queensland, Cairns-Atherton, and Cape York. Those inhabiting the last-named district are obviously recent arrivals from New Guinea. *Ptilinopus regina* and *Chalcophaps indica*, inhabiting monsoon forests and coastal scrubs in the Northern Territory and rain forests in the east, are differentiated into distinctive eastern and northwestern isolates. *Ptilinopus alligator*, known only from the Alligator River, is a distinctive derivative of the Timor-Sumba species, *Ptilinopus cincta*.

Amongst the savannah woodland-grassland species, *Geophaps scripta* and *G. smithii*, inhabiting Arnhem Land and Cape York-eastern Australia, respectively, have developed specific differences. The small doves, *Geopelia striata* and *G. humeralis*, and the crested pigeon, *Ocyphaps lophotes*, have undergone differentiation in the savannah tract in the Hamersley area of Western Australia. *G. striata* and *G. humeralis* have developed morphologically distinct isolates in the savannah area of southern New Guinea. *G. striata* has a hybrid zone in northwestern Australia.

The rock pigeons of central and northwestern Australia require a combination of rocky outcrops, spinifex, and surface water (Mayr, 1951) — an exceptional habitat. They are broken up into morphologically differentiated isolates to a surprising extent. *Lophophaps plumifera* has no fewer than 3-4 (see figure in Mayr, 1951), distributed as follows: (a) Midwestern Aus-*fera*) (this form extends across the continent to western Queens-district, at mouth of the Fitzroy River (*mungi*); (c) West Kimberleys (middle Fitzroy and Margaret Rivers) (*proxima*); (d) Middle Victoria River and Eastern Kimberleys (*plumifera*) (this form extends across the continent to western Queensland); (e) Central Australia (*leucogaster*).

These forms are apparently isolated from each other, the barriers separating them (sand plains) being terrain deficient in the basic requirements.

The genus *Petrophassa* contains two distinctive forms, *albipennis* and *rufipennis*, respectively isolated in the rugged gorges of the Kimberleys and Alligator River section of Arnhem Land. They are approaching, or have reached, that degree of differentiation typical of species.

In contrast to the above cases, there are several Australian Columbae that either do not vary geographically or else have only minor size or colour clines. These include: (a) *Phaps elegans,* an inhabitant of the southern and southeastern coastal fringe that has undifferentiated isolated populations in Tasmania and southwestern Australia. The population of *Leucosarcia melanoleuca* isolated in the Cairns rain forest may also prove to be undifferentiated. (b) *P. chalcoptera*, a large pigeon with a continent-wide range and that is essentially sedentary (and hence might be expected to vary). (c) A couple of eastern rain forest nomads (e.g. *Columba norfolciensis*), a highly nomadic interior species (*Histriophaps histrionica*), and a nomadic inhabitant of the northern coastal fringe (*Ducula spilorrhoa*).

Species with morphologically differentiated isolates beyond Australia are: *Chalcophaps indica*, 4 (plus an additional 4 to the *west* of Wallace's Line); *Ptilinopus regina*, 2-3; *Megaloprepia magnifica*, 3; *Ducula spilorrhoa*, 1; *Geopelia striata*, 3.

Order PSITTACI
Family PSITTACIDAE
(Parrots)

The Australian parrot fauna numbers about 50 species and, with the exception of half a dozen species obviously of northern origin (e.g. *Trichoglossus moluccanus, Opopsitta diophthalma, Probosciger aterrimus, Larius roratus*), is completely endemic. Radiation has been marked in all the basic ecological types.

These include: (a) somewhat generalized seed-eaters, inhabiting the wide areas of the continent covered by grassland savannah, (b) large heavy-billed cockatoos, that either eat the larger seeds and nuts, dig for roots, or else strip the bark from trees in search of wood-boring grubs, and (c) small, nectar-feeding lorikeets that exploit the large blossoms of the dominant *Eucalyptus, Grevillea,* and *Banksia* trees.

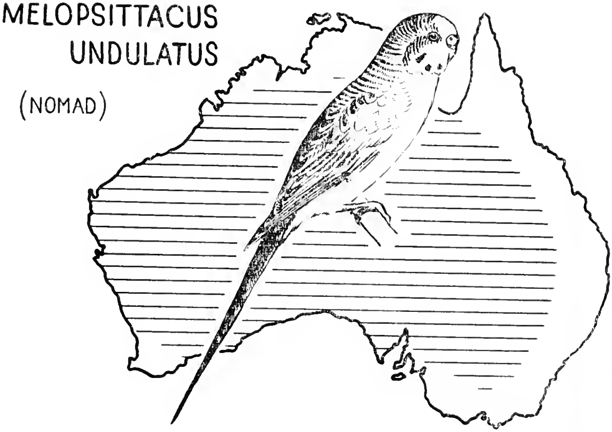

Fig. 9. The influence of nomadism on geographic variation. *Melopsittacus undulatus*, the domesticated budgerigah or ''parrakeet,'' is typical of the many interior species that are highly nomadic and breed wherever conditions are propitious. In none of the species with this form of seasonal behaviour does geographic variation or speciation occur.

The family Psittacidae is represented by species in all the major vegetation formations excepting mangroves and swamps. The majority of species are sedentary but nomadism is well developed in some of the inland grass-feeders, e.g. *Leptolophus hollandicus* and *Melopsittacus undulatus* (Fig. 9), and in many of the nectar feeders (*Trichoglossus* and *Glossopsitta*) that seasonally follow the flowering of the trees.

Speciation in Some Major Genera

As the various genera present a complicated variety of speciation situations they can best be reviewed individually.

Opopsitta: O. diophthalma, a rain forest fig-feeder, has three distinctive isolates confined, respectively, to the three major tracts of rain forest occurring in Australia (Fig. 10). Those populations inhabiting the two more southern tracts (*coxeni*, *leadbeateri*) have obviously been isolated for a considerable period of time for they are approaching the degree of differentiation typical of species. That inhabiting Cape York (*marshalli*), however, is presumably a recent immigrant for it is only doubtfully distinguishable from that inhabiting the Aru Islands.

Platycercus: The various species fall into two superspecies: *elegans-flaveolus-caledonicus* (Fig. 11), and *eximius-icterotis-adscitus-venustus* (Fig. 12).

The *P. elegans* group is fundamentally an inhabitant of the eastern coastal rain forests and mountain sclerophyll forests. In the Murray basin, however, in association with the development of morphological differences, one stock (*flaveolus*) has secondarily become adapted to inland riverside savannahs. Members of the *P. eximius* group inhabit savannah woodland and sclerophyll forest. They have much the wider range, with southwestern and northwestern representatives.

In *P. elegans* there is a distinctive isolate in the Cairns rain forest (*nigrescens*), and a Tasmanian isolate that is so distinctive that it is regarded as a species (*P. caledonicus*). The form inhabiting Kangaroo Island, at the western extremity of range, is similar to that of Victoria, but extending inland from the adjacent mainland is a chain of distinctive forms in which the dominant red pigment is gradually replaced by yellow (Condon 1941; Cain 1955). The forms, former isolates (?), are apparently connected by hybrid zones today. The end member (*flaveolus*), the most distinct, extends practically the entire length of the Murray. Towards the headwaters, however, it makes contact with typical *P. elegans* without interbreeding (Fig. 11). The situation thus is one of speciation by circle formation, the individual links of which are interfertile but the end members are not.[1] This is the only case of this type in Australian birds (Cain, 1955).

In the *P. eximius* group, inhabiting savannah woodland and sclerophyll forest there are major forms in the southeast (*P.*

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[1] One hybrid bird has since been found in the overlap area.

eximius), southwest (*P. icterotis*), northeast (*P. adscitus*), and northwest (*P. venustus*) of the continent, respectively (Fig.

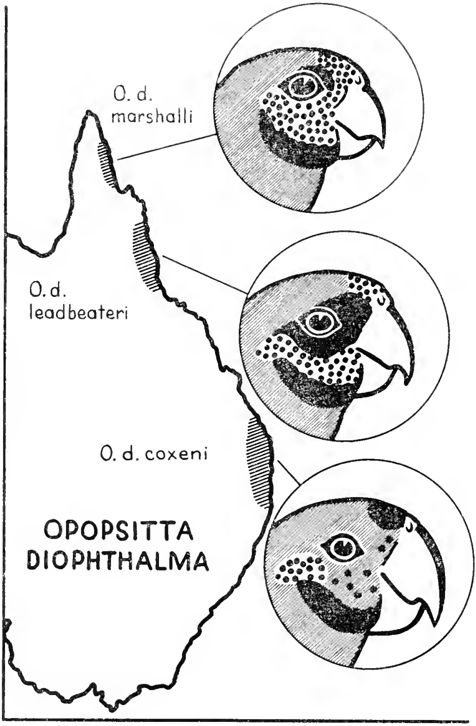

Fig. 10. Isolation and speciation in the rain forest fig-parrot, *Opopsitta diophthalma*. There is a distinctive form corresponding to each of the three major rain forest tracts in Australia.

Note differences in bill size and in the distribution of the red (spotted) and blue (black) areas on the head.

Rain forest species are often represented by distinctive forms in each of the three large tracts (New South Wales — southern Queensland, Cairns-Atherton and Cape York).

12). They obviously originated in these sections and from there spread out into the ranges they occupy today. Isolation remains complete in all instances except between *P. adscitus* and *P. eximius* where there is an area of overlap, in which some hybridization occurs. These major forms are so distinct morphologically that they can only be called species, although further study of the relationship of *P. eximius* and *P. adscitus* is required.

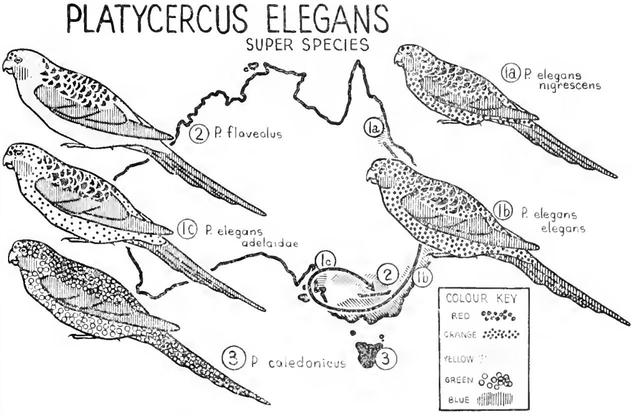

Fig. 11. Isolation and speciation by "circle formation" in rosella parrots of the *Platycercus elegans* superspecies. Distinctive isolates occur in the Cairns-Atherton rain forests (*elegans nigrescens*) and on Tasmania (*caledonicus*). These are indicated by "Ia" and "3" on the map, respectively. *P. elegans* proper (1b) extends through the sclerophyll forests of the eastern coastal strip. In southeastern South Australia, however, it is genetically connected, through a chain of interfertile forms (e.g. *P. e. adelaidae*—"1c") and hybrid zones, with *flaveolus* inhabiting the riverside savannahs of the Murray-Murrumbidgee River system ("2"). Towards the headwaters of these streams *flaveolus* and *elegans* make contact without interbreeding.

Within the four species, minor isolates occur on Tasmania (*P. eximius diemenensis*) and, currently or formerly, in various parts of coastal Queensland (e.g. Cape York, Cairns-Atherton area, Bowen area) in *P. adscitus*.

Barnardius: Speciation is also marked in this genus. As suggested by the map of Gentilli (1949), it is probable that *B. zonarius* originated in the southwest and *B. barnardi* in the east of the continent, respectively, at a time of greater aridity than today. Subsequently, *B. zonarius* has been able to extend to the east, crossing the Nullarbor Plain. Cain (1955) indicates that hybridization between the two occurs today in the vicinity of the Flinders Range.

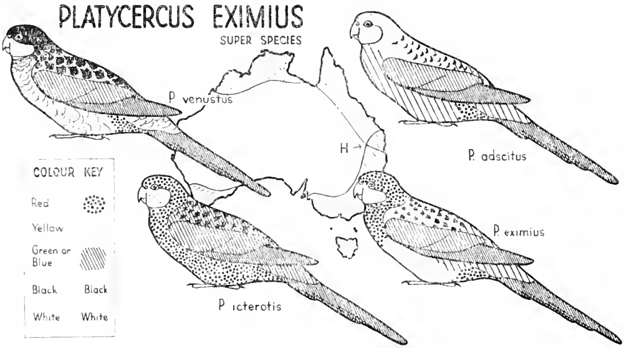

Fig. 12. Isolation and speciation in the *Platycercus eximius* group of savannah woodland — sclerophyll forest rosella parrots. Geographically-representative forms, so distinctive that they are called species, occur in the northwest, northeast, southeast, and southwest of the continent, respectively. Secondary range contact and some hybridization ("H") occur between *P. adscitus* and *P. eximius* today. The status of these forms requires further investigation.

P. eximius has a minor insular isolate on Tasmania.

The most interesting feature of *Barnardius* is that a series of distinctive isolates have developed in the various river systems in different parts of the continent. There are such forms centred on the group of rivers entering the head of the Gulf of Carpentaria in the north (*b. macgillivrayi*), the Hamersley (mid-western) watershed (*z. occidentalis*), the Murchison River (*z. connectens*), the southwest (*z. semitorquatus*), the streams arising in the Macdonells in central Australia (*z. myrtae*), and the Murray-Darling system (*b. barnardi*). The distribution of the group is essentially a "refuge" one.

Psephotus: This genus of 5 to 6 species falls into three species groups, representing earlier and later phases of radiation and speciation. These, and the vegetation formations they now occupy, are as follows: (a) *P. haematogaster* (with 5 subspecies, a couple of which are undoubtedly isolates), southern inland Australia (areas of savannah grassland, mallee, and mulga); (b) *P. haematonotus* (little geographic variation), inhabiting the temperate savannah woodland of southeastern Australia; (c) *P. varius* (savannah grassland and mulga), and the *P. chrysopterygius* superspecies (tropical savannah woodland mainly), including *P. c. chrysopterygius* on Cape York, *P. c. dissimilis* (Arnhem Land), and *P. pulcherrimus* (central and southern Queensland).

Speciation is actively occurring in the *P. varius-chrysopterygius* group, several isolates of which have reached the stage of morphological distinctness typical of species. The group has essentially a "refuge-type" distribution and the distribution of forms corresponds closely to that in the *Platycercus eximius* and other groups. These are: southeast of continent, in this case the Murray-Murrumbidgee system mainly (*P. varius orientalis*), southwest (*v. varius*), Arnhem Land (*chrysopterygius dissimilis*), Cape York (*c. chrysopterygius*), and eastern Queensland (*pulcherrimus*) — see distribution map in Cain (1955, Fig. 13). Of these *v. varius* has spread outward to central Australia and the Hamersleys.

Psephotus demonstrates a common phenomenon in Australian birds (*vide Climacteris, Platycerus*), namely, that where members of a genus live in close proximity to each other over an extensive area (including occupying adjacent habitats), they typically belong to *different* species groups. Alternatively, expressed, *within* each species group the members tend to be geographically representative, or else geographic overlap is only partial (more recent). The different rates at which differentiation and speciation may occur from one species group to another is also seen in *Psephotus,* in one group (*P. haematonotus*) there being no geographic variation, whereas in the others it is well advanced.

Neophema: Again there are three species groups, representing an earlier stage of radiation and speciation, plus a series of more recent forms. The species groups are: (a) *N. bourki* (inhabiting the arid interior, mainly mulga desert), (b) *N. chrysogaster — chrysostomus—elegans—petrophila* (southern riverside savannah woodland and dry sclerophyll forest, mostly), and (c) *N. pulchella-splendida* (southern dry sclerophyll-savannah woodland, and desert scrub, respectively).

It is within the second species group that much speciation has taken place. *N. chrysogaster* is fundamentally Tasmanian, though it now coexists with other members of the species on the mainland, and *N. elegans* probably originated in the southwest. It too occurs now in the southeast. *N. petrophila*, confined to the rocky coastline and offshore islands of the southwest and south, has the most unusual habitat and breeds in rocky crevices, not in trees. *N. chrysostoma* possibly originated in the interior (especially in the mallee areas) of the southeast. *N. pulchella* and *N. splendida*, making up the third group, isolated in the southeast and east and in the desert areas of southern Australia, respectively, also occupy dissimilar habitats.

Speciation in the Psittacidae, Summarized

Within the 32 members of this group covered, there are two instances of secondary range overlap by recently evolved species: the contact between *Neophema chrysostomus* and *N. elegans*, and the contact between the former and *N. chrysogaster* in southeastern Australia. In *Platycercus elegans-flaveolus* the end members of a chain of interfertile forms meet without interbreeding.

Isolates that have reached, or are approaching, that stage of morphological differentiation typical of genetic species occur as follows: *Opopsitta* (2), *Platycercus* (3), *Psophotus* (about 3), *Neophema* (about 2). There are some 13 morphologically differentiated isolates of lesser degree.

Hybrid zones occur between *Platycercus eximius* and *P. adscitus* and between *Barnardius zonarius* and *B. barnardi.*

The only parrots that do not vary at least somewhat geographically are nomads and those with restricted ranges. *Melopsittacus undulatus* and *Leptolophus hollandicus*, the first ranging widely over the continent (see Fig. 9), are examples of the former. Clines occur in continuously ranging species, e.g. *Kakatoe roseicapilla.*

Most species are confined to the continent and hence isolation and speciation is intra-continental. A couple of New Guinea species, however, have undifferentiated isolates on Cape York, e.g., *Larius roratus* and *Geoffroyus geoffroyi*. There is an interesting tendency in several parrot genera for river systems to act as refuges and for differentiation to occur within them.

Order CORACIAE

Families CORACIIDAE, ALCEDINIDAE, MEROPIDAE

(Rollers, Kingfishers, Bee-Eaters)

Only one roller (*Eurystomus*) and one bee-eater (*Merops*) occur in Australia, and both are south-north migrants, wintering in the islands to the north of the continent.

The Australian kingfishers number ten species and range from small four-inch long river kingfishers (*Alcyone*) to large forest kingfishers (*Dacelo*) a foot in length. The majority of species have had a northern origin but four are Australian.

Most are sedentary but south-north migration occurs in *Halcyon sancta*, *H. macleayi*, and *Tanysiptera sylvia*. The only true inland form, *H. pyrrhopygia*, is nomadic.

The various species fall into several well defined groups:—*Alcyone* (2 species), short-tailed diving forms; *Dacelo* (2) large forest forms and true endemics; *Halcyon-Syma* (5), forest and mangrove inhabitants, three of which are certainly recent immigrants with two (*H. chloris* and *H.* (*australasiae*) *sancta*) belonging to widely ranging Asio-Pacific species groups; *Tanysiptera* (1), long-tailed tropical kingfishers of New Guinea origin.

Speciation

Neither the roller, *Eurystomus orientalis*, nor the bee-eater (*Merops ornatus*) varies geographially in Australia.

Speciation in the kingfishers is limited to a series of isolates, as follows: (a) *Dacelo leachii*, inhabiting the northern savannah woodlands (isolates in the Gascoyne — De Grey segment of northwestern Australia), (b) *Syma torotoro* and *Tanysiptera sylvia*, restricted to Cape York, which populations are differentiated from the parental New Guinea species; (c) *Alcyone azurea* and *Halcyon macleayi*, river and savannah woodland species, respectively, differentiated into Arnhem Land and eastern forms. There is also a fair measure of isolation between the Australian and New Guinea forms in *Alcyone azurea*, *Halcyon macleayi*, and *Alcyone pusilla*. The small Cape York form (*minor*) of *Dacelo novaeguineae*, an eastern and southern sclerophyll forest-savannah woodland species, almost certainly developed in isolation. The Tasmanian and Mount Lofty populations of *Alcyone azurea* are undifferentiated isolates.

A hybrid zone occurs in *Alcyone pusilla* in the Gulf of Carpentaria-Cape York area.

Size and colour clines occur in several species. In *Dacelo leachii* the Torres Strait barrier has led to a reversal of the species south-north size cline, the New Guinea population having a longer wing than the one on the adjacent mainland.

The nomad *Halcyon pyrrhopygia* and the migrant *H. sancta* have only negligible variation in Australia.

Beyond Australia, *Halcyon chloris* has some 40 morphologically differentiated isolates in a range from Africa to Polynesia. *H. australasiae*, of which *H. sancta* is a derivative, has a dozen or more. *Alcyone* and *Syma* have various forms in New Guinea.

Order PASSERES

Families MENURIDAE AND ATRICHORNITHIDAE

(Lyrebirds and Scrub-birds)

The lyrebirds (*Menura*), large, ground-living, long-tailed forest inhabitants fall into two species, one inhabiting the Macpherson Range, and the other the coastal forests of the east and southeast. The equally unique scrub-birds (*Atrichornis*), requiring dense undergrowth, are confined to eastern Australia (*A. rufescens*) and southwestern Australia (*A. clamosus*) — see map in Chisholm (1951).

All members of the group are sedentary species.

Speciation

Atrichornis falls into the common pattern of an evolving group being severed into an eastern and a southwestern component, the latter, *A. clamosus*, which has become extinct since settlement, being very distinct.

Menura alberti, the only bird species to be confined to the Macpherson Range rain forests, probably originated there for the area is obviously a refuge of long standing. *M. novaehollandiae* has presumably secondarily spread from the south, for it now reaches southern Queensland. It has, moreover, given rise to a distinct (? isolated) form (*edwardi*) in the Stanthorpe granite belt.

Family CAMPEPHAGIDAE
(Cuckoo-Shrikes)

The eight species that constitute the Australian Campephagidae include both older endemic forms and recent colonizers. The most interesting of the former is *Pteropodocys maxima,* a ground-feeding species of the dry interior, which is partly nomadic. Most species, by contrast, occupy a somewhat generalized food niche — the larger insects of the branches and foliage.

The endemic *Coracina robusta* of southern Australia and its "advanced" northern counterpart (*C. papuensis*), that lacks the immature plumage phase, obviously represent two distinct invasions from the north. *C. novaehollandiae,* the Australian populations of which are the end members of a chain of forms extending from India through Indonesia, has had a long period in Australia for it is broken up into several distinct forms here and has secondarily colonized New Caledonia to give rise to a new species there, *C. caledonica. Lalage sueurii* possibly originated in Australia for the endemic race (*tricolor*) is unique in having an eclipse plumage (Mayr, 1940b) and is well adapted to the dryer parts of the continent.

The remaining cuckoo-shrikes (*Coracina lineata, C. tenuirostris,* and *Lalage leucomela*) are fairly recent colonizers of the Australian continent from the north.

Speciation

Morphologically differentiated isolates occur in the Australian Campephagidae, as follows: *Coracina novaehollandiae,* inhabiting sclerophyll forest and savannah, 2, possibly 3 (one well differentiated); *C. papuensis,* tropical savannah woodlands, 2, possibly 3, all minor forms; *C. tenuirostris,* sclerophyll and savannah woodlands, 1 (probably), a minor form; and *Lalage leucomela,* rain forest fringes and mangroves, 2 or 3. The total of 7-10 continental isolates contrasts with 35 in those species (*C. papuensis, C. lineata, C. tenuirostris,* and *L. leucomela*) inhabiting an archipelago area in the southwest Pacific of equivalent size, and 48-49 for the whole island area east of Wallace's Line.

The ecological characteristics of this family relative to their tendency to undergo isolation and differentiation, have previously been discussed (Keast, 1958 i). Geographic variation tends to be absent or negligible in species occupying habitats that are broad as well as long (i.e. of an "inland" type), and that are continuous. It is suppressed in interior nomadic species, of which *Lalage tricolor* and *Pteropodocys maxima* are the main examples. South-north migrants, however, may vary geographically and even have isolates, e.g. *Coracina novachollandiae* and *C. tenuirostris*.

Clines occur in various species. *C. novachollandiae* has, in addition to a south-north cline of decreasing wing length, one of increasing bill length.

Family MUSCICAPIDAE
Subfamily MUSCICAPINAE
(Flycatchers, Fantails, and Whistlers)

This subfamily is made up of a mixture of Australian and New Guinea elements. Thus, of the four species of *Rhipidura*, *leucophrys* and possibly *fuliginosa* are Australian, and the other two are of tropical origin. The monotypic genus *Seisura* is Australian, whilst *Piezorhynchus*, *Machaerirhynchus*, *Arses*, *Monarcha*, *Heteromyias*, and *Tregellasia*, obviously originated in New Guinea or the adjacent islands. *Myiagra*, *Microeca*, and *Pachycephala*, are well developed both in the tropics and in Australia. The robin-like flycatchers (*Petroica*, *Eopsaltria*) are, by contrast, Australian, as are *Falcunculus* and *Oreoica* in the *Pachycephalini*.

The flycatchers are forest dwellers, with rain forest and sclerophyll forest being richest in number of species. A few are south-north migrants. The movements are partial (restricted to some populations) in *Rhipidura rufifrons*, *Myiagra rubecula*, *Monarcha melanopsis*, and *Pachycephala rufiventris*, and more general in *Petroica rodinogaster* (from Tasmania) and *Myiagra cyanoleuca*.

Speciation

The various flycatcher species differ widely in the extent and significance of their geographic variation. There are some three cases of recently completed speciation, various well differentiated isolates, a variety of minor isolates, and a couple of minor hybrid zones. Several species have striking colour and size clines. Others, however, do not vary at all geographically.

(a) Instances of Recently Completed Speciation

Petroica rodinogaster: This species is an insular (Tasmanian) derivative of *P. rosea*. *P. rodinogaster*, however, now migrates across Bass Strait to winter, and sometimes breeds, alongside the Dandenong Range population of its parent. The two behave to one another as good species.

Petroica vittata: This is an insular (Tasmanian) isolate of *P. cucullata* that, in dropping the pied male plumage of its parent form and reverting to a brown "henny" plumage, has

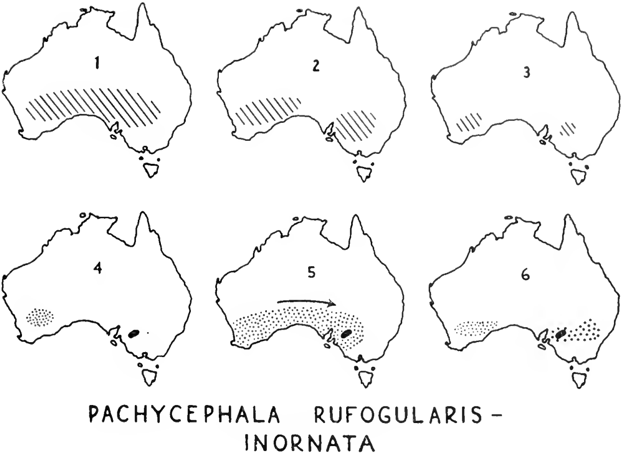

Fig. 13. Speciation in the *Pachycephala inornata* — *P. rufogularis* group of mallee thickheads, a suggested hypothesis.

The distribution of species and races today are as shown in the final map with *P. rufogularis* (see black ellipse) being confined to a restricted section in western Victoria. *P. inornata* is isolated into western (*inornata inornata*) and eastern (*gilberti*) races, indicated by light and heavy stippling, respectively.

It would seem likely that a widely ranging parental form (map 1) became split and isolated in the western and eastern sections of the continent, respectively (maps 2 and 3), there to build up genetic differences (map 4). Subsequently, *P. inornata* colonized eastwards, to co-exist with P. *rufogularis*. More recently, in accordance with the severence of the mallee habitat, the former has become broken up into eastern and western isolates.

The hypothesis presupposes south-north shifts of the rainfall belts causing vegetational changes.

undergone marked differentiation. It remains isolated, however, though specific distinctness can certainly be assumed.

Eopsaltria georgiana and *E. australis* (race *griseogularis*): This is a case of speciation by double invasion into the forested corner of southwestern Australia, the former being the older stock.

Pachycephala rufogularis: This species occupies a very restricted range in the Victorian mallee, where it coexists with the eastern form of its near relative, *P. inornata.* There would seem to be little doubt that the two developed in the eastern and western mallee tracts, respectively, when the parental stock became severed into two (Fig. 13). *P. inornata* was subsequently able to extend eastwards again to coexist with, and spread much wider than the essentially relict *P. rufofularis.*

(b) Morphologically Differentiated Isolates

Isolates so distinctive that they must be considered to be approaching the degree of differentiation typical of species are:

(i) The Arnhem Land and Cape York populations of the monsoon forest robins, *Poecilodryas superciliosa* (*cerviniventris* and *superciliosa*).

(ii) The southwestern and southeastern populations of the sclerophyll savannah woodland robin, *Eopsaltria australis* (*griseogularis* and *australis*).

(iii) The northwestern and northeastern forms of the mangrove whistler, *Pachycephalia simplex* (*simplex* and *peninsulae*).

(iv) The northwestern, southeastern, and southwestern forms of the sclerophyll-savannah woodland shrike-tit, *Falcunculus frontatus* (*whitei, frontatus, leucogaster*).

The total number of morphologically differentiated isolates in the Muscicapinae will be seen from Table 5 to be 31-35. They occur in the following species, whose habitat is also given:

Rhipidura fuliginosa, various habitats, 4-5, one of which is well differentiated; *R. rufifrons,* rain forest, 1, well differentiated; *Seisura inquieta,* savannah woodland, 2, one major, one minor; *Piezorhynchus alecto,* mangroves and rain forest, 2, one major, one minor; *Myiagra rubecula,* sclerophyll forest, 1, minor; *Machaerirhynchus flaviventer,* rain forest, 1, minor; *Monarcha trivirgata,* rain forest, 1, major; *Microeca leucophaea,* savannah and sclerophyll, and *M. flavigaster,* tropical savannah woodland, 1 each, both minor; *Petroica multicolor,* sclerophyll forest, 1, minor; *Eopsaltria australis,* sclerophyll forest and savannah, 2, one major, one minor; *Poecilodryas superciliosa,* monsoon forest, 1, major form; *Tregellasia capito,* rain forest, 1, minor; *Pachycephala pectoralis,* various habitats, 5-7, minor and major forms; *P. inornata,* mallee, 1, a minor form; *P. lanioides,* mangroves, 3, minor forms; *P. simplex,* mangroves, 1, major form; and *Falcunculus frontatus,* sclerophyll and savannah woodland, 2, major forms.

In addition to the above there are several cases of isolation without differentiation in the Muscicapinae, e.g. *Petroica chrysoptera* and *P. multicolor* in Tasmania.

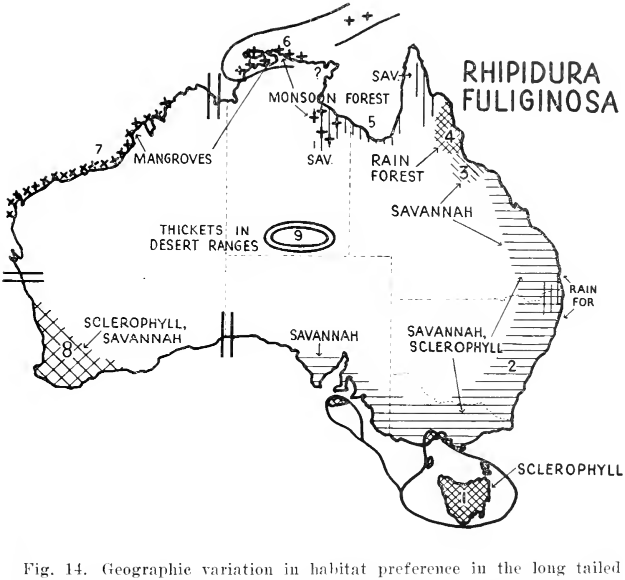

Fig. 14. Geographic variation in habitat preference in the long tailed flycatcher *Rhipidura fuliginosa.* This species, with essentially a peripheral range, occupies different habitats in various parts of the continent. This form of ecological variation indicates how, simultaneously with the development of genetic and morphological characters, isolates can become specialized for life in vegetation formations different from that occupied by the parental form.

The numbers 1-9 on the map indicate races and isolates. The pairs of parallel lines represent distributional barriers (see Keast, 1958a).

Note the isolate (9) in the mountains of central Australia.

Rhipidura fuliginosa (Fig. 14) and *Pachycephala pectoralis* provide interesting examples of geographic variation in the vegetation formation occupied, coincident with the acquisition of geographic morphological differences. In different parts of the range they inhabit rain forest, sclerophyll forest, savannah woodland, mangroves (and in the case of the latter even mallee) — see Section XII.

Colonization by New Guinea rainforest species across Torres Strait has been the main way in which new flycatchers have been added to the Australian avifauna, the group being best developed in the tropics. Various stages of differentiation from parental New Guinea stocks occur in Cape York in the different species.

Three recent colonizers, confined to the northern tip of the Peninsula, have yet to differentiate: *Monarcha frater*, *Microeca griseoceps* and *Tregellasia leucops.* In *Monarcha trivirgata*, an immigrant New Guinea stock (*albiventris*) occupies the northern part of this peninsula and a well-differentiated Australian form (*gouldi*) the southern part. They possibly meet and hybridize. In *Machaerirhynchus flaviventer,* the descendents of an earlier wave of colonization are now isolated in the Cairns-Atherton rain forests (*secundus*) and the later ones on northern Cape York (*flaviventer*). In the genus *Arses* there is a similar situation but in this case the earlier form is now so distinctive that, though still isolated, it must be regarded as having reached species status (*A. kaupi*). The later invader, *A. telescopthalmus*, has itself now differentiated from the parental New Guinea stock (race *lorealis*).

There has been some reverse colonization of the savannah woodland areas of southern New Guinea by Australian species, the following having given rise to distinct isolates there: *Rhipidura leucophrys* (race *melaleuca*), and *Microeca leucophaea* (*zimmeri*).

Hybrid zones do not occur in the flycatchers except for some minor ones in *Pachycephala pectoralis* (Mayr, 1954a).

There are no nomadic species amongst the Australian flycatchers. Four species, however, have migratory populations in the southeast part of their range. This partial migration has not prohibited the development of geographic variation in these species, two of them having morphologically differentiated isolates (*Rhipidura rufifrons* and *Myiagra rubecula*), and two varying clinally (*Pachycephala rufiventris* and *Monarcha melanopsis*).

Size and colour clines are developed in most sedentary Australian flycatchers that have, on the one hand, an extensive

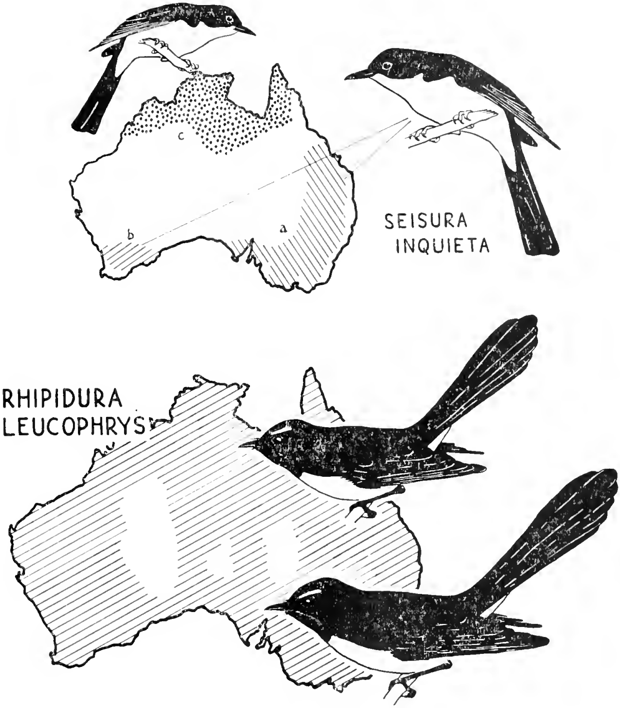

Fig. 15. The influence of isolation on south-north clines of decreasing size. Bergmann's Rule has a wide application in Australian birds. In the continuously ranging *Rhipidura leucophrys* southernmost and northernmost populations differ in size by 11 per cent.

In *Seisura inquieta,* however, in which there is a gap in the range, the difference is 22 per cent (see Keast, 1958a).

The letters a, b, and c indicate isolated populations of *S. inquieta.*

south-north range and, on the other, range through areas of widely differing rainfall. Thus, size clines occur in *Rhipidura leucophrys*, *Petroica cucullata*, and *Myiagra rubecula*. *Seisura inquieta* (Fig. 15) provides an interesting demonstration of the effects of isolation on a south-north size cline. Southernmost and northernmost populations in this species differ in size by about 22 per cent, the range gap being in northeastern Queensland. In the comparable *Rhipidura leucophrys*, in which the range is continuous, it amounts to only 11 per cent.

Speciation and radiation in the islands of the southwest Pacific are taking place in three "Australian" flycatcher species (Table 5). These are: *Rhipidura rufifrons* (Mayr and Moynihan, 1946), which has some 20 morphologically differentiated isolates, *Petroica multicolor* (Mayr, 1934), with about 12, and *Pachycephala pectoralis* (Galbraith, 1956) with over 50. The last-named is the richest of all bird species in number of races (Mayr, 1954a, p. 11). In addition to the above, the genus *Petroica* has given rise to many island forms in the New Zealand area (Fleming, 1950).

Subfamily TIMALIINAE
(Babblers)

The seven members of the Tribe Cinclosomatini covered in the present review are all inhabitants of the heavily forested regions except for the arid-country *Sphenostoma cristatum* and the mallee species *Drymodes brunniopygia*.

Speciation

Psophodes is composed of two species, one (*P. olivaceus*) restricted to the rain forest and sclerophyll forest regions of the eastern seaboard and the other the "ecologically-versatile" (*P. nigrogularis*) inhabitating the sclerophyll and mallee of the southwest, with an isolated relict race in the eastern mallee tract (*leucogaster*). Keast (1958g, Figs. 1 and 2) has suggested a series of steps, associated with major climatic oscillations, reflected also in *Pachycephala inornata-rufogularis*, to explain speciation in the genus. These are: (a) a parental stock formerly ranging right along the southern seaboard; (b) isolation of the stock into eastern and western populations as the result of climatic deterioration, and/or edaphic changes; (c) ecological and morphological modification of the western population, the result of its being more exposed to the harsh environment; (d) eastward colonization of the western mallee-adapted form, now specifically distinct (*P. nigrogularis*); (e) isolation of *P. nigrogularis* into eastern and western forms as a result of the mallee becoming divided into two tracts.

Psophodes is interesting in that it demonstrates a pathway of adaptation from life in the luxurious coastal forests to that in the semi-arid mallee. There is evidence that the southwest has also given rise to dry-country forms in other bird groups.

The genus *Drymodes* has a surprising distribution, one species inhabiting the southern mallee and the second (basically a New Guinea one) the rain forests of Cape York. The latter has, moreover, a minor isolate some 400 miles to the west on the Roper River (*colcloughi*), the only bird species to have an outlyer confined to this section. The origin of this race, like the circumstances of the original isolation of the species themselves, is obscure.

Orthonyx is composed of two species, *O. temminckii* and *O. spaldingii*. The former has a surprising pattern of distribution, the rain forests of eastern Australia from the Illawarra district, New South Wales, to the Bunya Mountains, Queensland (with minor range gaps) and then reappearing, as a distinctive colour form, 1500 miles to the north in New Guinea. *O. spaldingii* is confined to the Cairns-Atherton rain forest tract.

The monotoypic *Sphenostoma cristatum* shows only clinal variation.

Subfamily SILVIINAE
(Old World Warblers)

The only Australian representatives of this Palaearctic subfamily (Mayr and Amadon, 1951) are *Megalurus* (2 species), *Acrocephalus* (1), and *Cisticola* (2). *Acrocephalus* and *Cisticola* are Ethiopio-Palearctic genera.

Speciation

The swamp-dwelling *Megalurus gramineus* has minor isolates in Tasmania and in the southwestern corner of Western Australia, but *M. timoriensis,* despite an extensive peripheral range, does not vary geographically in Australia (Keast, 1956b).

Acrocephalus arundinaceus has distinct western and eastern forms, whilst there is also possibly an isolate in the Kimberleys (Mayr, 1948). *Cisticola* is represented by two species, both of which have a wide extra-Australian range and are only secondarily Australian. One of these, *C. exilis*, has some four colour forms within the continent and possibly fairly complete isolation as between the populations inhabiting the east and northwest of the ranges (Lynes, 1930; Keast, unpublished). The other, *C. juncidis*, has isolated, differentiated populations in the Normanton and Darwin areas respectively.

Subfamily MALURINAE
(Australian Warblers)

In contrast with the Muscicapinae almost all the members of the Malurinae occurring in Australia originated within the confines of the continent. Those genera that are restricted to Australia are *Epthianura*, with its monotypic derivative *Ashbyia* (5 species), *Acanthiza* (10 species, plus one in the mountains of New Guinea), *Amytornis* (7 species), *Malurus* (7 species, plus one in New Guinea), *Smicrornis* (monotypic), *Aphelocephala* (3 species), *Pyrrholaemus* (monotypic) *Hylacola* (2 species), *Calamanthus* (2 species), *Cthonicola* (monotypic), *Origma* (monotypic), *Pycnoptilus* (monotypic), *Cinclorhamphus* (2 species), *Dasyornis* (2 species), *Stipiturus* (2 species), *Acanthornis* and *Oreoscopus*, the last two monotypic derivatives of *Sericornis*.

Gerygone (9 Australian species) and *Sericornis* (5 species) are equally developed in New Guinea and Australia. The island, for its part, has several endemic genera that are close relatives of those occurring in Australia (e.g., *Todopsis*).

The Australian warblers are all small, basically insectivorous, species. They inhabit either the foliage or ground and low undergrowth, with most genera being specialized toward one or the other zone. *Acanthiza* and *Sericornis*, however, have representatives in both zones. Those that live in the undergrowth are mostly characterized by long upturned tails, e.g. *Malurus*, *Amytornis*, *Stipiturus* and, to a lesser extent, *Hylacola*. The Australian Malurinae total 62 species.

Speciation in the Major Genera

A number of the Australian "sylviid" genera provide excellent demonstrations of speciation within the confines of the continent. They can best be considered individually.

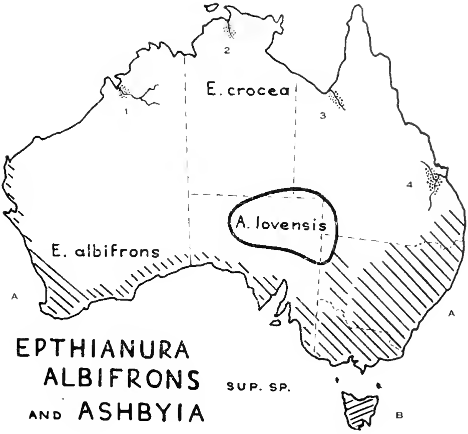

Fig. 16. Distinctive relict races of the chat, *Epthianura crocea* (numbers 1-4 and spotted areas on map) are isolated in river valleys 800-900 miles apart. Distribution of this species, requiring dense ground cover and submarshy conditions, can only be explained by the north of the continent formerly having been wetter and providing continuous, or near-continuous, habitat of the right type.

The black ellipse indicates the range of *Ashbyia lovensis,* an inhabitant of the gibber deserts. Though fairly sedentary, its range is continuous and restricted. It does not vary geographically.

Epthianura albifrons (see cross-hatched areas) is somewhat nomadic on the mainland (see A) and does not vary geographically. Interruption to gene flow by Bass Strait, however, has led to the development of a minor insular isolate on Tasmania (B).

Epthianura and *Ashbyia:* This group, reviewed in detail elsewhere (Keast, 1958c), demonstrates the close link between the type of seasonal movements undertaken by species and their tendency to develop morphologically differentiated isolates. Of the five species, *Epthianura crocea* is unique in being sedentary, widely ranging, and in having highly specialized habitat requirements. It has four isolated and well differentiated populations in river valleys, respectively 600, 700, and 800 miles apart in the north of the continent. *E. albifrons*, somewhat nomadic and with a coastal and inland distribution varies only in the insular Tasmanian population. *E. aurifrons*, habitat generalized, distribution interior (i.e., wide and continuous), nomadic but movements varying with area and seasonal conditions, has no geographic variation. *E. tricolor* has a generalized habitat and a continuous interior distribution. It is markedly nomadic and with a seasonal shift in abundance from south to north of continent. Breeding habits must accelerate gene flow. There is no regular breeding area but it breeds wherever conditions happen to be suitable. It may breed in autumn in centre and north of continent as well as in spring in south and it is a colonial nesting species. No geographic variation occurs. *Ashbyia lovensis* is restricted to arid gibber desert in centre of continent, a continuous but moderately restricted habitat. It is fairly sedentary. There is no geographic variation.

The number of morphologically differentiated isolates in the Australian chats is thus four. Three of these are in *Epthianura crocea* (Fig. 16).

Gerygone: Nine of the 15 species in this genus occur in Australia and they fall into perhaps 5 species groups. Three of these (*G. palpebrosa*, *G. magnirostris*, and *G. chloronota*) are of New Guinea origin. Within Australia the various species are adapted to habitats ranging from tropical rain forest to coastal woodlands, mangroves, and the arid interior. They are typically sedentary forms but two species, *Gerygone olivacea* and *G. fusca*, have (south-north) migratory races.

Speciation is actively occurring in the genus. *G. olivacea*, a sclerophyll forest-savannah woodland species, has isolates in north Queensland (a minor form), the northwest (*rogersi*), and southern New Guinea (*cinerascens*). The New Guinea *G. hypoxantha*, known only from Geelvink Bay, could be an early isolate of this species. The rain forest species *G. palpebrosa* is broken up into three fairly distinctive stocks, inhabiting the tracts of this association on Cape York (*palpebrosa*), Cairns-Atherton (*johnstoni*), and Mackay-Rockhampton (*flavida*). A second rain forest species, *G.* (*igata*) *richmondi* has isolated stocks (minor races) in eastern New South Wales-southern Queensland (*richmondi*), the Bowen-Mackay area (*amalia*), and Cairns-Atherton area (*mouki*). The mangrove species, *G. laevigaster*, inhabiting the northern coastline from Derby to Normanton, is broken up into three minor forms inhabiting, respectively, the mangrove tracts in the following areas: Derby-Napier Broome Bay (*broomei*), Port Essington-Melville Island (*laevigaster*), and the Roper River-Norman River (*mastersi*). *G. cantator* of eastern Australia, a form approaching the degree of differentiation typical of a species, is apparently also a derivative of this stock. The distinctive infraspecific form *tenebrosa*, ranging from Carnarvon to King Sound, bears a similar relationship to the widely-ranging *G. magnirostris* (Meise, 1931).

G. c. chloronota of Arnhem Land is an Australian isolate of a New Guinea species.

There are thus some 10 morphologically differentiated isolates in the genus *Gerygone* within continental Australia.

A further interesting feature is that several of the "brown" species of *Gerygone* are relatively better differentiated on the basis of habitat and call notes than they are morphologically. This particularly applies to *G. richmondi*, *G. fusca*, and *G. laevigaster*.

Insular forms of *Gerygone* occur in New Zealand and on Lord Howe Island (*G. igata*).

Smicrornis: This monotypic genus lacks isolates but shows marked geographic colour variation, plus a minor south-north size cline. The occurrence of the colour forms in this species in broad belts from east to west across the continent shows an interesting correlation with rainfall and temperature. It has been suggested that specific climatic thresholds may operate to produce this rather interesting variation of the Gloger Effect (Keast, 1958h).

Aphelocephala: The three species in this genus are, respectively, inhabitants of arid gibber desert (*A. pectoralis* and *A. nigrocincta*) and savannah woodland-grassland (*A. leucopsis*). The gibber deserts, occurring mainly in two extensive south-north tracts, break up the savannah into eastern, central, and western sections, leading to minor isolates in the latter species. The others do not vary geographically.

Acanthiza: The thornbills extend widely over the continent. As many as five species may co-exist in an area (e.g., about

Sydney) but are nevertheless well differentiated ecologically, particularly in feeding zone and/or the sub-association occupied.

Acanthiza presents various interesting situations from the speciation viewpoint (Mayr and Serventy, 1938). There is a case of speciation by double invasion, *A. ewingi* and *A. pusilla diemenensis* representing successive waves of colonization of Tasmania. Well differentiated isolates that could be said to be approaching species status include *A. pusilla katherina* and *A. reguloides squamata* in northeastern Queensland.

The total number of morphologically differentiated isolates in *Acanthiza* (Table 3) is about 15, most of them minor forms.

In the sclerophyll and savannah woodland species isolates occur in: the Cairns-Atherton area (*A. pusilla katherina, A. nana flava*); central Queensland (*A. reguloides squamata*); Tasmania (*A. pusilla diemenensis, A. ewingi*); Mount Lofty area of South Australia (*A. reguloides australis, A. nana laetior, A. lineata clelandi*). There is a form of *A. pusilla* confined to Kangaroo Island (*zietzi*), and the population of *A. lineata* there (*chandleri*) agrees in colouration with that inhabiting Victoria, not the adjacent areas of South Australia. In addition to the above, *A. chrysorrhoa* has a well differentiated isolate in the region of the Gulf of Carpentaria (*normantoni*).

The distinctive colour types of *A. pusilla* and *A. chrysorrhoa* inhabiting southwestern Australia are of uncertain origin. They could represent western outlyers of forest stocks from eastern Australia, or be derived by local selection (the area is one of high rainfall) from adjacent dry country stocks (Mayr and Serventy, 1938; Serventy, 1953). However, the southwestern type of *A. pusilla* has secondarily extended right across the continent to New South Wales. In this section, accordingly, the coastal and interior races are quite distinct.

The interesting relict isolates of the ground-dwelling Samphire Thornbill (*A. iredalei*) inhabiting, respectively, the arid interior (*iredalei*), heath country in eastern South Australia (*hedleyi*), and samphire adjacent to St. Vincent's Gulf (*rosinae*), have been discussed by Condon (1954).

Attention is drawn by Mayr and Serventy (1938) to two noteworthy characteristics of the species *A. pusilla* and *A. chrysorrhoa*. They are particularly versatile ecologically, habitats being occupied that range from rain forest fringes with an annual rainfall of over 100 inches per annum, to savannah woodland, mallee, and mulga, in the 10-inch rainfall zone. Each is split up into a chain of wet, intermediate, and dry country races.

Sericornis: The rain forest-sclerophyll-savannah woodland superspecies *S. frontalis* is divisible into four basic forms which, in that they are largely isolated, may or may not be entitled to species status (Mayr, 1937). They inhabit the southwest (*S. maculatus*) and southeast (*S. frontalis*) of the continent, Tasmania (*S. humilis*), and Cape York — New Guinea (*S. beccarii*), respectively. *S. frontalis* and *S. maculatus* have given rise to a few hybrid individuals in South Australia (Mayr). *S. maculatus,* which occupies the dryer southwestern part of the continent, is broken up into 3-4 minor isolated forms, two of which occupy the Abrolhos and Recherche Island groups, respectively (Mayr and Wolk, 1953).

The rain forest species *S. citreogularis* and *S. magnirostris,* ranging from New South Wales to the Cairns-Atherton region, each have a minor isolate at the northern end of the range.

Hylacola: This genus contains two species so similar that they would be regarded as geographic races did they not occupy adjacent habitats in one restricted area. Of the two, *H. pyrrhopygia* is an inhabitant of heathy under-scrub within the sclerophyll formations of eastern and southeastern Australia. The other occupies this type of habitat in southwestern and South Australia, but in the eastern part of the range inhabits mallee. The contact zone, in the Bendigo area of Victoria, is where the two kinds of habitat come together.

Calamanthus: This genus is broken up into two stocks, a coastal one (*C. fuliginosus*) and an interior one (*C. campestris*), which differ significantly in size and colour. The two are largely isolated but intergrade in the Eyre Peninsula and Coorong section of South Australia, *C. campestris* moving down dry corridors into the coastal habitat of *C. fuliginosus.* The latter has minor isolates on Tasmania and in southwestern Australia.

Amytornis: This distinctive genus constitutes one of the few true desert groups in the Australian avifauna, the various species being basically inhabitants of *Triodia* (porcupine grass). Their habit is secretive and they keep low down. Dense continuous cover is the prime requisite. Distribution tends to be broken up into "pockets." Dispersive capacities are poor.

There are two species groups: *A. textilis* and *A. striatus.*

The genus is remarkable (Keast, 1958b) for: (a) Bizarre changes in bill-form, from that typical of an insect-eater to the heavy "seed-grinding," finch-like type occurring in the *A. textilis* group (Fig. 17). The degree of size and colour variation as between species in the *A. striatus* group (Fig. 18), is also exceptional. The two species groups exhibit evolutionary changes reminiscent of those seen in the Galapagos and Hawaiian archipelagos. (b) There are no fewer than 4 isolated populations, so distinctive morphologically that they must be genetic species, yet each known from only a single locality: *A. goyderi* (lower Macumba River, north of Lake Eyre), *A. dorotheae* (MacArthur River, Gulf of Carpentaria), *A. woodwardi* (Alligator River, Arnhem Land), *A. housei* (Charnley River, in the Kimberleys).

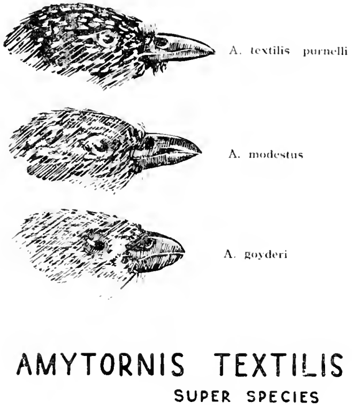

Fig. 17. Differentiation in bill form coincident with speciation in desert grass wrens of the *Amytornis textilis* group. The three species show successive stages in the transition from an insectivorous to a granivorous type of bill.

Amytornis provides one example of secondary overlap by newly evolved species: i.e., *A. modestus* and *A. textilis* in the Macdonnell Ranges. The two obviously originated in the east and west of the continent, respectively.

Geographic variation in the habitat occupied occurs in *Amytornis striatus* and *A. textilis* (Figs. 17a and 18a). The former, a widely distributed "parental" species occupying a range of habitats, has budded off a series of species around the periphery of its range that occupy rocky gorges only. In the *A. textilis* group there is the alternative situation of this species, occupying the western half of the continent, and the eastern *A. modestus*, each somewhat versatile in choice of habitat, separating out

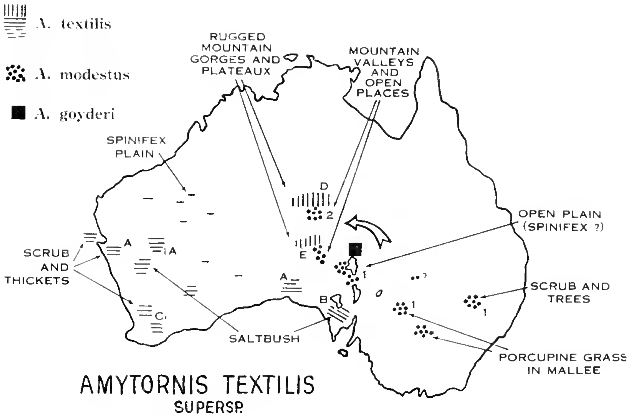

Fig. 17a. *Amytornis textilis* group of desert grass wrens. Distribution of species and their geographic variation in habitat is shown. The black square indicates the restricted range of the heavy-billed *A. goyderi* (now probably extinct.) *A. textilis* and *A. modestus*, relatively similar western and eastern counterparts, secondarily overlap in range (without interbreeding) in the mountains of central Australia. Each frequents a range of habitats except in the overlap zone, where one keeps to the rugged gorges and the other to the valleys. Here *A. modestus* is probably the secondary invader.

The letters refer to minor racial forms of *A. textilis*, and the numbers to those of *A. modestus*.

where their distributions meet. Thus, in the Macdonnell Ranges in central Australia, the former keeps to the rock surfaces of the gorges and plateaux and the latter to the areas of soft spinifex on the valley floor.

The isolated derivatives of *A. striatus* (*A. dorotheae*, *A. woodwardi*, and *A. housei*) could only have reached their present range at a time when desert (spinifex) replaced savannah grassland (an unsuitable habitat in that it lacks permanent cover).

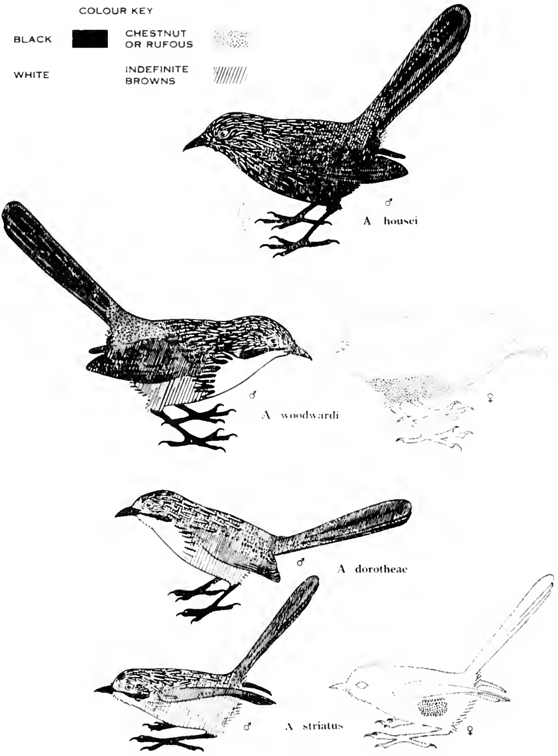

Fig. 18. Members of the *Amytornis striatus* superspecies to show the acquisition of striking size and colour differences. Though isolated, these forms have diverged morphologically to such an extent that there can be little doubt that they are genetic species.

Dasyornis: The two species, *D. broadbenti* and *D. brachypterus,* whose habitat is dense coastal undergrowth, have a discontinuous and relict distribution, each being isolated into two distinctive stocks, a southeastern and a southwestern one (see figure in Keast, 1957b). The southwestern forms are virtually extinct today.

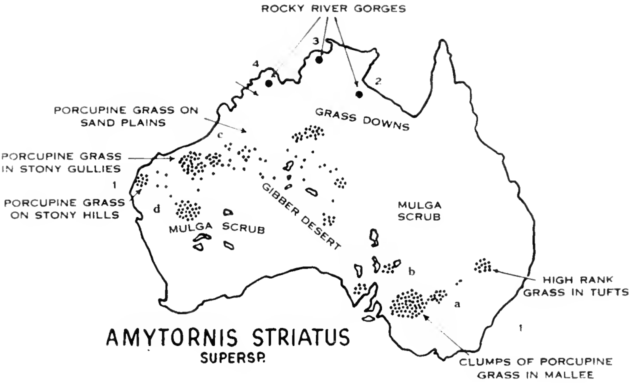

Fig. 18a. The range of the various forms in the *A. striatus* superspecies. The parental *A. striatus* (1, a-d) extends widely through the arid and semi-arid interior, whilst the distinctive derivatives *A. dorotheae*, *A. woodwardi*, and *A. housei* (2, 3, 4) are isolated in the rocky gorges of the McArthur, Alligator, and Charnley Rivers, respectively. The habitats occupied in different areas are shown on the outside of the map, vegetation formations that constitute distributional barriers on the inside.

The three northern species could only have reached their present position at a time when desert spinifex grassland was continuous through to the northern seaboard.

Stipiturus: A single superspecies is involved here, there being three major, isolated, stocks falling into two species. Their distribution is shown in Figure 19.

Stipiturus is an interesting genus in two ways: (a) because of the large number (5) of morphologically differentiated isolates in the species *S. malachurus.* These, occupying shrinking areas of specialized coastal habitat and cut off from the main stock in southeastern Australia, occur as follows:— Tasmania (*littleri*), Kangaroo Island (*halmaturinus*), Mount Compass area of South Australia (*intermedius*), southwestern Australia (*westernensis*), and Dirk Hartog Island (*hartogi*). (b) It provides an interesting demonstration of an ecological transition

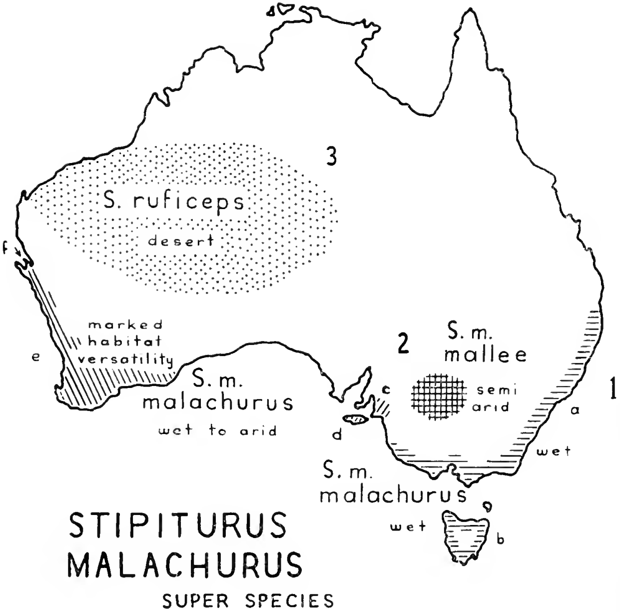

Fig. 19. Isolation, speciation, and habitat differentiation, in emu-wrens of the genus *Stipiturus*. *S. malachurus* (1), a secretive species requiring dense undergrowth, is broken up distributionally into a series of minor isolates around the periphery of the continent (see a-f).

Distributional barriers are areas of open country and sea. Distinctive isolated forms, approaching or that have reached species status (*S. malachurus mallee* — 2, and *S. ruficeps* — 3), occur in semi-arid and arid mallee and spinifex desert areas, respectively.

Eastern populations of *S. malachurus* are limited to sub-marshy areas, but in the southwest, where coastal undergrowth and spinifex lie in close proximity, adjacent populations demonstrate the complete ecological transition to life in arid places.

from life in well watered coastal areas to that in arid spinifex desert.

The three forms occupy quite distinct habitats: *S. malachurus*, submarshy coastal heathlands and thickets (basically), *S.(malachurus) mallee*, the mallee, and *S. ruficeps*, desert spinifex. *S. malachurus* does, however, vary geographically in the habitat occupied. In coastal New South Wales, Victoria, and Tasmania, submarshy areas of rank grass and heath (40-inch rainfall zone) are inhabited. On Kangaroo Island the habitat is dry undergrowth, including thickets on stony hills (25-inch rainfall zone). In the southwest of the continent the species extends from the coastal regions out through the regions of semi-arid to arid scrub and undergrowth towards the 10-inch rainfall isohyet.

Malurus: This genus with 12 Australian species forms a compact group. All are sedentary, somewhat gregarious, and occupy habitat of the shrub or rank grassland type in different parts of the continent. Speciation is actively occurring.

Malurus falls into five species groups: *M. cyaneus-melanotus-callainus-splendens*, *M. lamberti*, *M. leuconotus*, *M. melanotis*, and *M. coronatus*. The first two are particularly interesting from the viewpoint of speciation.

Malurus cyaneus-melanotus-callainus-splendens group of wren species (Fig. 8). These forms occupy broad, mutually exclusive zones and different habitats, from east to west across the continent. Three of the four have reached that stage of colour pattern differentiation typical of genetic species. The habitats occupied, however, the common denominator of which is dense shrubby cover, could be described as being as distinct in terms of vegetation type and climate as "proven" species in other genera. The only possible zone of contact between the four forms, however, is in New South Wales, where riverside thickets (occupied by *M. cyaneus*) and mallee (occupied by *M. melanotus*) approach each other. The relationship between habitat occupied and speciation in this and other groups is discussed in Section VII.

Within the *M. lamberti* group, distinct forms occupy the following areas of the continent (Fig. 20): (a) arid interior of continent (*mastersi*), (b) well-watered coastal fringe of New South Wales (*lamberti*), (c) mallee and creekside thickets in western New South Wales (*assimilis*), (d) high-rainfall coastal corner of southwestern Australia (*elegans*), (e) "intermediate" country in southwestern Australia and on Eyre Peninsula (*pulcherrimus*), (f) tropical Cape York (*amabilis*), (g) tropical northwestern Australia (*dulcior*). In addition there is a minor colour isolate on Bernier Island, northwestern Australia (*bernieri*).

Since the seven geographically representative forms largely replace each other, and have diverged only a minor to moderate extent morphologically, there has long been doubt as to their status. A field study in southwestern Australia by Serventy

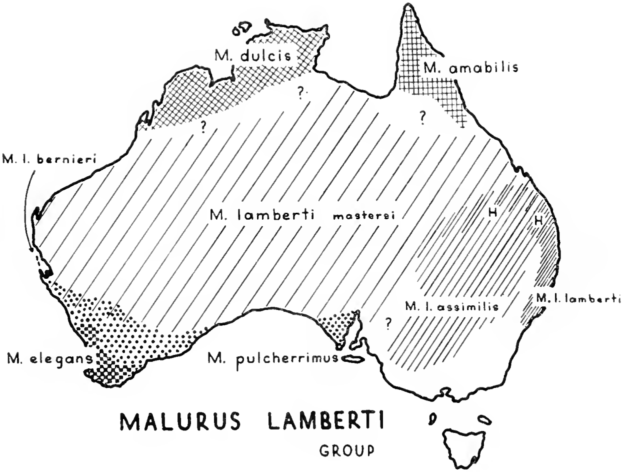

Fig. 20. Distribution of species and forms in the *Malurus lamberti* group of chestnut-shouldered wrens. Speciation and variation in this group are highly complex and incompletely understood.

In the southwest of the continent three distinctive colour forms, occupying adjacent zones behave as good species to each other. These are: *Malurus elegans, M. pulcherrimus,* and *M. lamberti mastersi.* Three colour forms in the east, also occupying zones of decreasing rainfall, intergrade where they meet (see H). These are the races *M. lamberti lamberti, M. l. assimilis,* and *M. l. mastersi.*

Two distinctive forms in the northwest and northeast of the continent are isolated from each other and, apparently, from the desert *mastersi.* Their genetic status is unknown but, in view of the fact that they differ to as great a degree as *elegans, pulcherrimus,* and *lamberti,* they are best regarded as taxonomic species.

The group thus contains three proven species, and possibly five.

(1951), however, has surprisingly demonstrated that the three forms occurring there (*elegans, pulcherrimus, lamberti mastersi*), despite being fairly similar in colour, overlap in range and behave as good species toward each other. In contrast with this situation, the three morphologically and ecologically equivalent forms in the east (*lamberti lamberti, l. assimilis, l. mastersi*) intergrade in southern Queensland where the dry country approaches the coast (Mack, 1934b). This contact is probably secondary.

The Cape York and Arnhem Land representatives of the group (*amabilis* and *dulcior*) live in relatively wet areas and are apparently isolated from the desert *mastersi* by a considerable range gap, deficient in ground cover. They are at least as distinct morphologically from each other and from *mastersi* as are *elegans* and *pulcherrimus*.

The evolutionary situation in the chestnut-shouldered wrens is thus a highly interesting one. There are three proven species, plus two isolated forms sufficiently distinct morphologically to suggest that they could not successfully interbreed.

The zonal nature of the distribution of *M. elegans, M. pulcherrimus,* and *M. lamberti mastersi*, in southwestern Australia is presumably a secondary phenomenon. *M. elegans* could, conceivably, have come from the east, colonizing around the coastline. *M. pulcherrimus* has an outlyer on Eyre Peninsula (i.e., like the other southwestern species *Climacteris rufa* and *Eopsaltria australis* [*griseogularis*].

The other species groups in *Malurus* have one morphologically differentiated isolate each, as follows: *M. leuconotus* (one on Dirk Hartog and Barrow Islands), *M. melanocephalus,* a species with an eastern and northern coastal distribution (one in northwestern Australia), and *M. coronatus* (one, possibly, in the country at the head of the Gulf of Carpentaria).

Speciation in the Subfamily Malurinae, Summarized

There are three instances of secondary range overlap by "newly evolved" species: *Acanthiza ewingi* — *A. pusilla diemenensis* in Tasmania, and *Malurus elegans* — *M. pulcherrimus* — *M. lamberti mastersi*, in southwestern Australia.

Isolates that have reached such a stage of morphological differentiation that they must be good genetic species occur as follows: *Gerygone*, 2; *Amytornis*, 4; *Stipiturus*, 1 or 2; *Malurus*, 4-5. Total: 11-13.

Morphologically differentiated isolates of lesser degree total 61 (Table 3), 16 of which could be said to have reached a moderate stage of differentiation. This is over one per species. It reflects the relatively poor dispersive capacities of the majority, their local habits, tendency to keep to dense cover, and fairly specific habitat requirements.

Hybrid zones occur in *Sericornis maculosa-frontalis*, and between the eastern forms in the *Malurus lamberti* complex.

Some 23 malurinid species do not vary geographically, but some 21 of these have such restricted ranges that this would not be expected, e.g., *Acanthiza ewingi*, *Origma rubecula*, and *Oreoscopus gutturalis*. The remaining two (*Epithianura tricolor* and *E. aurifrons*) are nomads.

Colour and size clines occur in several malurinid species, especially in those belonging to the genus *Acanthiza*. *Smicrornis brevirostris* has both. In the genus *Amytornis*, however, coincident with speciation, these trends may be reversed.

Gerygone magnirostris, *G. palpebrosa*, and *G. chloronota*, that extend through to New Guinea, have minor isolates in that region.

Family ARTAMIDAE
(Wood-Swallows)

The six Australian Wood-Swallows (4 of them endemic) are aerial feeders and hence are strong on the wing. Most of them range widely over the continent.

Speciation

The development of geographic variation in this group in association with seasonal movements has been reviewed by Keast (1958c). In only the single sedentary species (*A. cinereus*) is it marked, but isolation is lacking. Two migratory species have minor clinical variation, *A. leucorhynchus* and *cyanopterus*. The remainder, strongly nomadic species, do not vary at all geographically.

A. leucorhynchus, in an extra-Australian range extending from the Andamans and Philippines to Fiji and Palau, has some 9 distinctive isolates.

Family SITTIDAE
(Nuthatches and Australian Tree-Creepers)

This family, as now constituted (Mayr and Amadon, 1951), contains two genera in Australia, *Climateris* and *Neositta*, ecological counterparts, respectively, of the creepers and nuthatches of the Palaearctic. The species are highly specialized ecologically, gaining their insect food from fissures and cracks in the trunks and branches, though some members of *Climacteris picumnus* group have taken secondarily to feeding from the ground. *Climacteris* has six species in Australia, one extending to New Guinea. *Neositta* is now regarded as being composed of only one species (Mayr, 1950b — See Figure 21).

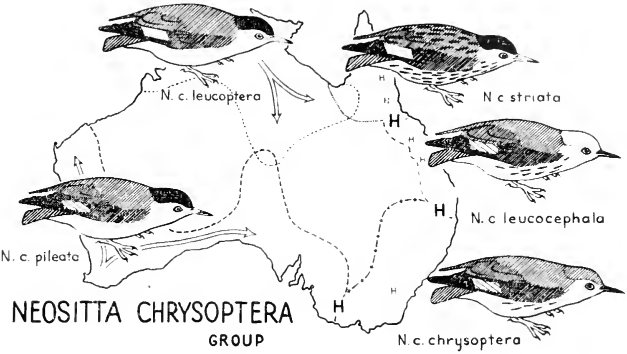

Fig. 21. *Neositta chrysoptera* superspecies, a case of multiple hybridization at contact fronts (Mayr, 1951). In this case distinctive forms have developed in various parts of the continent, including the southwest, northwest, Cape York, central Queensland, and southeast. Secondarily, however, outward extension of range has occurred, particularly from the northwest and southwest (see white arrows). Zones of hybridization (see letters H) connect a number of the forms today.

Neositta is significant in two ways: as an example of multiple hybridization, and in that relatively great morphological differences have been attained without reproductive isolation. Thus, head colouring may be brown (indicated by close cross-hatching), black, or white. Body striations may be absent. The bill may be black or yellow. The wing bar may be orange (sparse cross-hatching) or white.

Climacteris has species in a range of habitats but *Neositta* is essentially a species of sclerophyll forests and savannah. All species are sedentary.

Speciation

Climacteris is composed of three species groups (Keast, 1957e). Most interesting of these is the *C. picumnus* group of savannah woodland species and forms (Fig. 22). *C. picumnus* proper inhabits the southeast and its distinctive isolate, *C. picumnus melanotis*, the northeast. *C. rufa*, an isolate so distinctive that it must be regarded as having reached species status, occupies the southwest and has a minor derivative on Eyre Peninsula. *C. melanura* inhabits the northwestern sector and has a derivative (*wellsi*) in the Hamersley section of the central west. There

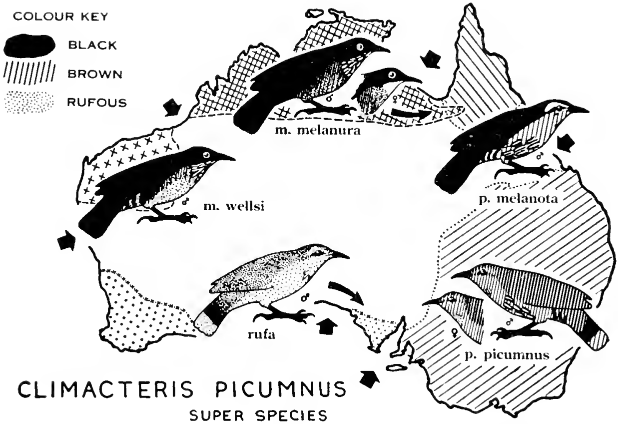

Fig. 22. Isolation and speciation in the *Climacteris picumnus* group of savannah-dwelling tree-creepers. There is a distinctive form corresponding to each of the major savannah woodland belts on the continent. In contrast with *Neositta*, though there has been outward range spread, secondary contact has occurred only in the north. Here, however, there is no hybridization, showing that specific distinctness has been attained.

The southwestern form, *C. rufa*, can, in view of its distinctiveness, best (from the taxonomic point of view) be regarded as a species.

The black arrows on the outside of the map indicate the distributional barriers, each a dry to arid section from which the necessary habitat is absent. The arrows within the map indicate major secondary range extensions.

is thus a chain of six forms, each centred on a hilly or mountainous "refuge" area. All remain isolated except at the head of the Gulf of Carpentaria where *C. melanura* has secondarily extended its range to meet and co-exist with *C. picumnus melanotis*, without interbreeding. Within the group there is, accordingly, the full range of stages in the speciation process from minor isolates to a newly-evolved species.

C. leucophaea, making up the second species group is a montane species in New Guinea (3 isolates), and a rain forest-sclerophyll forest species in eastern Australia. Here it has two morphologically differentiated isolates, a distinctive one in the Cairns-Atherton region (*minor*), and a lesser one in the Mount Lofty Ranges (*grisescens*). The third species group is composed of two species, *C. erythrops* (inhabiting mountain sclerophyll in the east) and *C. affinis* (mulga desert).

Climacteris provides one of the best demonstrations of differentiation and speciation in refuge areas. These same tracts of country also function as refuge areas in other groups, e.g. parrots, nuthatches.

Neositta provides a most interesting contrast with *Climacteris* in that (though differentiation has again occurred in these refuge areas) the various isolates have secondarily reunited to form hybrid zones (Mayr, 1950b). The genus has a chain of forms around the periphery of the continent, as follows: southeast (*chrysoptera chrysoptera*), southwest and south (*pileata*), northwest and north (*leucoptera*), northeast (*striata*), central east (*albata, leucocephala*, etc). *Neositta* provides a splendid example of multiple hybridization (intergradation) along contact fronts (see Section X), and is surprising for the degree of differentiation achieved without the attainment of reproductive isolation. The morphological characteristics, ranges, and approximate areas of hybrid zones in *Neositta* are shown in Figure 21. Differentiation of forms has occurred in the same areas as in *Climacteris*, except that *Neositta* lacks them in the Hamersley and Eyre Peninsula sectors and has several in eastern Queensland.

Clinal variation occurs in various Australian Sittidae.

Family DICAEIDAE
(Flower-seekers and Pardalotes)

This family, in Australia, falls into two genera, the endemic and somewhat aberrant *Pardalotus* (7 species) and *Dicaeum* (1 species). The latter is well developed in southeastern Asia, Indonesia, New Guinea, and islands of the western Pacific. *Dicaeum hirundinaceum*, the Australian representative, is itself the end member of a superspecies extending through from Asia.

Pardalotus occurs throughout Australia. *P. punctatus* inhabits the sclerophyll forests of eastern and southern Australia and has given rise to *P. quadragintus* in Tasmania and to the mallee species, *P. xanthopygus*. *P. melanocephalus* mainly inhabits the tropical savannah woodlands. *P. rubricatus* is a savannah grassland-arid country species. The remaining species live in dry sclerophyll forest and savannah woodland, with a distinct tendency to occur along rivers. *Dicaeum hirundinaceum* occurs throughout the continent and has an extremely wide habitat tolerance.

Dicaeum is highly nomadic. *Pardalotus striatus* has a south-north migration. Other pardalotes, inhabiting the dryer areas, are apparently partial nomads.

Speciation

Pardalotus contains an instance of speciation by double invasion (into Tasmania), *P. quadragintus* representing the earlier, and the endemic race of *P. punctatus* (*leachi*) the later one. Apart from this, the only differentiating isolates in the group are the insignificant southwestern form of *P. punctatus* and the northwestern one of *P. melanocephalus*.

The puzzling status and relationships of *Pardalotus substriatus*, *P. ornatus*, and *P. striatus*, largely geographically representative forms recognizable only on minor grounds, have been discussed by Hindwood and Mayr (1946) and Serventy (1953). The first of these extends widely across the southern two-thirds of the continent, the second through a broad south-north zone in the east, and the third is confined to Tasmania and the southeastern coastal strip of the mainland. The three overlap in eastern Australia but, despite their morphological similarity and the absence of habitat differences between them, only 1.8 per cent of the specimens are morphologically intermediate, i.e. hybrids, according to the findings of Hindwood and Mayr. Serventy (1953), however, interprets the evidence differently, saying that *ornatus* is itself nothing but a hybrid form. He also draws attention to the existence of a specimen from southwestern Australia that has a yellow wing speculum (a characteristic of the southeastern *striatus*) as indicating the presence of occasional genes of that species in the far west. Serventy suggests that all the "striped-crowned" pardolates, hence, probably belong to a single species. In any event, there can be little doubt that *P. substriatus* originated in southwestern Australia and *P. striatus* in Tasmania. A high proportion of the latter occurring in eastern Australia are winter migrants.

P. melanocephalus is the northern representative of the group. It obviously originated in the northwest or north and has secondarily spread southwards to overlap the range of *P. substriatus.*

The ecology of *Dicaeum hirundinaceum*, its intimate relationship with the mistletoes (Loranthaceae), and the influence of these on its potential for developing geographic variation have been discussed by Keast (1958d). *Loranthus* berries form the main food of *Dicaeum*, and the bird undertakes extensive seasonal movements coincident with the fruiting of the plants. This may be in spring, summer, autumn, or winter, in different areas. Its breeding is also linked to the berry crop. The occurrence of mistletoes in all the main forest and scrub associations explains the wide range of vegetation formations inhabited by *Dicaeum*. The bird is a major disseminator of *Loranthus*.

D. hirundinaceum has only negligible geographic variation in Australia. Where, however, the nomadic habit has been lost (i.e., in the colonizing of the Aru, Kei, and Tenimber Islands), distinctive insular isolates occur.

Family MELIPHAGIDAE
(Honeyeaters)

This is an Australo-Papuan family of about 150 species, some 67 of which occur in Australia. Their common character is the brush-tongue and, though primarily insectivorous, nectar is prominent in the diet.

Of the 20 or more genera occurring in Australia, 12 obviously originated here: *Melithreptus, Plectorhynchus, Certhionyx, Acanthorhynchus, Gliciphila, Ramsayornis, Granticlla, Conopophila, Zanthomiza, Phylidonyris* (with *Meliornis*), *Manorina* (with *Myzantha*), and *Anthochaera-Acanthagenys.*

At the species level all are apparently Australian with the exception of about 18 that are recent immigrants from New

Guinea, or are obviously derived from such. The majority of the 23 species of the large genus *Meliphaga* occurring in Australia are endemic.

Honeyeater species are specialized for life in the full range of vegetation formations and the degree of "habitat tolerance" of any one is commonly limited. Many species are sedentary but "blossom nomadism," of limited amplitude, is widespread. A few species, especially *Grantiella picta*, *Certhionyx variegatus*, *Myzomelia nigra*, are highly nomadic. *Meliphaga chrysops* and *Melithreptus lunatus* are partial south-north migrants in the southeastern part of their range.

Speciation

The Australian Meliphagidae contain examples of a wide range of speciation phenomena, including two instances of triple invasion, one of re-invasion, and several demonstrations of secondary range overlap by recently evolved species. There are a considerable number of minor instances of isolation and differentiation.

(a) Instances of Recently Completed Speciation and some Special Phenomena

(i) *Melithreptus lunatus* and *M. albogularis*, a case of secondary range overlap in peripheral sclerophyll-savannah woodland species (Fig. 23). These two species are so similar that, if they did not co-exist over an extensive area, they would rank as no more than minor geographic races. Both are strictly peripheral in range, inhabiting sclerophyll forest and savannah woodland. *M. lunatus* is southern and eastern in distribution, *M. albogularis* northern and eastern. The overlap area extends from Cairns to the Richmond River, a distance of 1,000 miles (Fig. 23).

Interest in this case lies in: (a) circumstances of the original isolation and hence speciation; (b) how it is possible for two such similar species to co-exist.

There can be little doubt that *M. albogularis* developed in the Kimberley-Arnhem Land sector of the northwest, that is to the west of the Gulf of Carpentaria. A recent eastward extension of range by various northwestern bird species and races has been noted (Keast, 1956a). *M. albogularis*, however, has followed this with a great range extension southwards through the coastal forests of eastern Queensland.

Fig. 23. Speciation in the *Melithreptus lunatus* group of savannah woodland — sclerophyll forest honeyeaters.

M. lunatus (1 — stippled areas) is related to the others as follows: *M. albogularis* (2—see cross-hatching), barely distinguishable on morphological grounds, mainly inhabits the north of the continent but overlaps the range of *M. lunatus* in eastern Australia by about 1,000 miles. *M. affinis* (3 — range shown in black), is a distinctive Tasmanian isolate. *M. lunatus chloropsis* (4 — heavily spotted area), a long-billed isolate in the southwest, has reached a lesser degree of divergence.

There can be no doubt that the sibling species *M. albogularis* originated in northwestern Australia (or possibly even New Guinea) and that its occurrence in eastern Australia is secondary. In at least part of the overlap area it occupies a different habitat to *M. lunatus*.

M. lunatus and *M. albogularis* occupy slightly different areas in the overlap zone. The former occurs only on the tops of the ranges and the latter only in the lowlands (Barnard and Barnard, 1925; Barnard, 1926). Several other southern bird species are restricted to the higher country in the northern parts of their range, e.g., *Meliphaga lewini* and *Dacelo novaeguineae*. In colonizing southwards, *M. albogularis* may accordingly have been able to move, partly unimpeded by competition, through the lowlands.

The fleshy orbital ring is a vivid orange colour in the eastern race of *M. lunatus*. In other members of the genus, and in the southwestern race of this species, this area of the body is a drab white, greenish, or pale blue colour. The character could have an important role in helping to prevent hybridization with the superficially similar *M. albogularis*.[1]

(ii) *Meliphaga lewini*, *M. notata*, and *M. gracilis*, a case of triple invasion by rain forest species from New Guinea (Fig. 24). These three species have the same colouration and colour pattern and obviously are derived from a common New Guinea stock. The chief differences are in size, *M. lewini* being the largest and *M. gracilis* the smallest, and in the relatively long bill of *M. gracilis*. *M. lewini* does not have a close counterpart in New Guinea, whereas *M. notata* shares a semi-species relationship with *M. analoga* there (Rand, 1936), and *M. gracilis*, in Australia, is only racially distinct from its parental form.

M. lewini, the species with the southernmost range (Dandenongs to the Cairns-Atherton area), has obviously had a fairly long history in Australia. By contrast, the bifurcation of *analoga-notata* from *gracilis* must have taken place in New Guinea. *M. notata* and *M. gracilis* are now each broken up into two populations in Australia, inhabiting the Cape York and Cairns rain forests, respectively.

Where the three species overlap, *M. lewini* occupies the highlands and *M. notata* the lowlands (Barnard, 1926). The long-billed *M. gracilis* is also a lowland dweller.

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[1] Brown and Wilson (1956) might regard this as an example of a character being modified as the result of contact between two closely related species. Against this, however, is the argument that the red orbital ring is typical of *M. lunatus* throughout its eastern range, not just where it meets *M. albogularis*. There would seem to be no doubt that the latter is the invader.

Actually there is relatively little evidence of modification to, or reinforcement of, a morphological character in zones of contact between closely related species in Australian birds — though see *Meliphaga virescens-versicolor*.

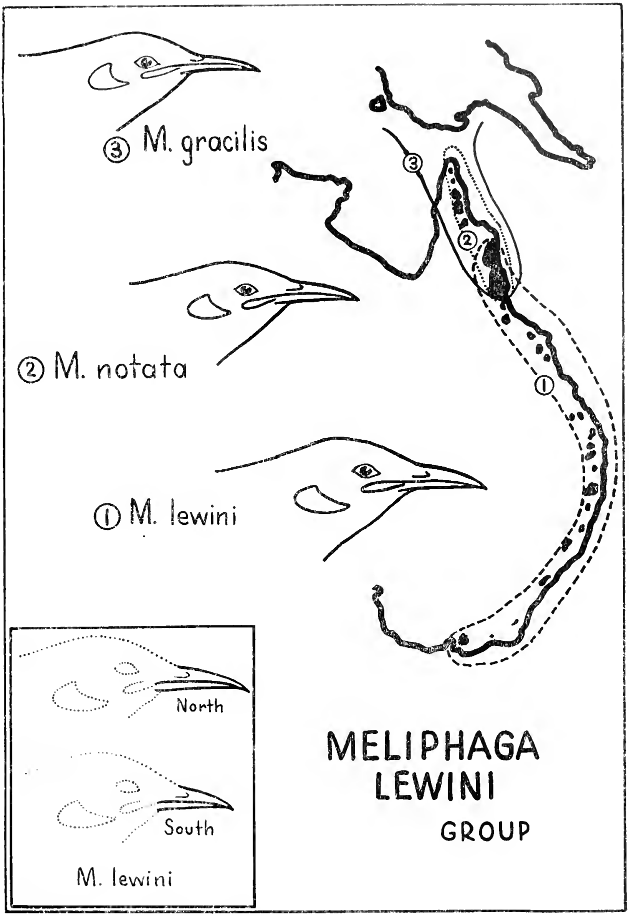

Fig. 24. Triple invasion of Australia by similarly coloured New Guinea rain forest honeyeaters of the *Meliphaga lewini — notata — gracilis* group. The distinctive endemic species *M. lewini* (1) obviously represents the first wave. *M. notata* (2), the second arrival, ranks as a semi-species with *M. analoga* of New Guinea. *M. gracilis* (3), the most recent arrival, is only racially distinct from its New Guinea parent.

M. lewini and *M. notata* occupy different sub-zones where they overlap, the former keeping to the highlands and the latter to the lowlands. *M. lewini* has a south-north cline of increasing bill length and decreasing wing length.

(iii) *Meliphaga virescens* and *M. versicolor*, a case of speciation in New Guinea and reinvasion of the Australian continent into a new habitat (Fig. 25).

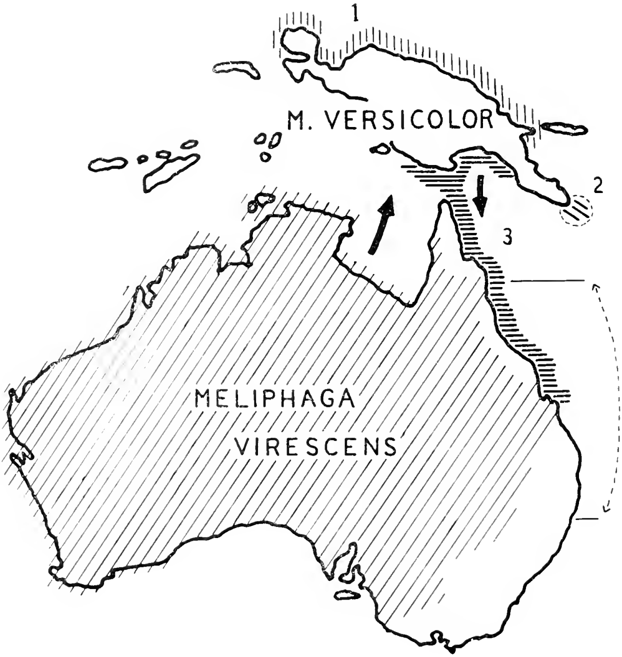

Fig. 25. *Meliphaga virescens* superspecies, a case of speciation by "reinvasion." The parental species has a wide range through the arid interior of Australia. It only enters mangroves in the west where conditions are dry. The New Guinea derivative, *M. versicolor*, has re-invaded the continent (see black arrows) to colonize the unoccupied eastern mangroves. It does not go beyond the forest fringes adjacent to the mangroves and hence has a range parallel to, but not overlapping, that of *M. virescens*.

The dotted arrows indicate the range of an earlier specialized derivative, *M. fasciogularis*, a species inhabiting the more southern mangroves of eastern Australia.

The numbers indicate geographic races of *M. versicolor*.

M. virescens, a widely ranging savannah grassland-mulga species, varies clinally in colour and size. *M. versicolor* has three forms, one inhabiting northern New Guinea that is barely distinguishable from typical *virescens*, one in the Milne Bay area that is intermediate, and one in southern New Guinea and Cape York that has accentuated colouring and is markedly distinct from *virescens*. Nevertheless, all would rank as one species were it not for the fact that *M. virescens* and *M. versicolor* occur together, without interbreeding, on Cape York.

M.versicolor obviously represents a branch of *M. virescens* that became isolated in New Guinea and there built up genetic and morphological differences from the parental stock. The habitat relationships of the two are interesting. *M. virescens* extends throughout the dry parts of the continent but does not penetrate into the wet eastern coastal strip. In the dryer west, however, it does occupy mangroves. On Cape York it is confined to the dryer savannahs of the western side. *M. veriscolor*, a coastal species in New Guinea, has invaded Australia into the offshore mangroves of eastern Cape York.

The mangroves of southeastern Queensland are occupied by a third related species, *M. fasciogularis*. This is isolated from *M. virescens* by the wet coastal forests but overlaps *M. versicolor* in range without interbreeding.

(iv) *Philemon argenticeps* and *P. novaeguineae*, a case of triple invasion from New Guinea (Fig. 26).

The friarbird *Philemon* (*moluccensis*) *novaeguineae* has a wide distribution through the islands to the north of Australia. It has invaded the Australian continent three times, the earliest wave giving rise to the savannah dwelling *P. argenticeps*, and subsequent ones to *P. novaeguineae gordoni* and *P. n. yorki* in the mangroves (mainly) of Arnhem Land and coastal savannah woodlands of Cape York, respectively. The degree of morphological distinctness of the forms is only moderate and were it not for their co-existing they would only rank as races (Mayr, 1944a, p. 167). *P. argenticeps*, the earliest arrival, is now well adapted to the dry country and extends well south into it.

(v) Dry country *Meliphaga* species of the *cratitia-plumula-ornata-keartlandi-flavescens-fusca* groups, examples of "refuge area" differentiation and speciation.

These species fall into two or three species groups, the members of each of which tend to occupy different segments of the fairly

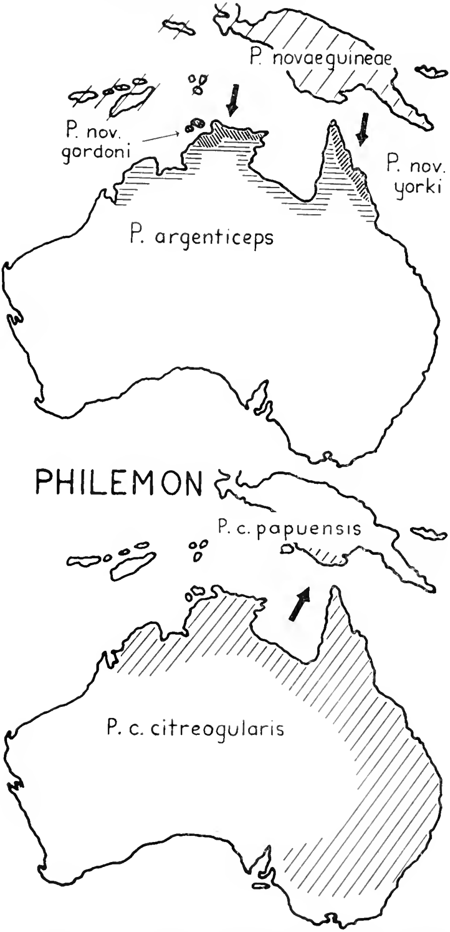

Fig. 26. Speciation in the genus *Philemon* (Meliphagidae). *P. novaeguineae* has invaded Australia from the north three times. The first colonization (now *P. argenticeps*), adapted to dry savannah forest, has reached specific distinctness, as shown by its non-hybridization with later arrivals. Subsequently, there have been parallel waves of colonization into the northwest and northeast, respectively (*novaeguineae gordoni* and *n. yorki*). The latter two keep to the mangroves and wetter coastal savanah.

The lower map demonstrates a case of the reverse process, colonization of the savannah woodland areas of southern New Guinea by the Australian savannah species, *Philemon citreogularis.* The insular population has now reached race status.

dry (mainly savannah woodland-grassland) parts of the continent. Their ranges, however, may be marked by broad overlaps today. Habitat differences are often present but ill-defined, with equivalent plant associations being occupied by different species as between north and south, or east and west.

Current distribution patterns indicate that species arose in the east (*fusca*), north (*flavescens*), and south (*cratitia*, *ornata*) of the continent.

(vi) *Myzantha flavigula* and *M. melanotis* in the Victorian mallee.

This puzzling case has been discussed by Serventy (1953). In southwestern Australia the widely ranging, savannah woodland-grassland *M. flavigula* is connected clinally with a darkly pigmented race in southwestern Australia (*obscura*), inhabiting the coastal high rainfall zone. In the Victorian mallee, however, where a similar colour form (*melanotis*) occurs, it behaves as a distinct breeding unit co-existing, but not hybridizing, with *M. flavigula*.

The circumstances of the original isolation of *M. melanotis* are obscure, unless the species is of southwestern origin.

(vii) The semi-species *Meliphaga melanops* and *M. cassidix*, secondary contact without interbreeding.

These two species are so similar morphologically that they can only doubtfully be distinguished in the field. *M. melanops* has a fairly wide range in the sclerophyll forests of eastern Australia and it approaches and apparently meets *M. cassidix* (restricted to the Dandenong region of Victoria), along the periphery of its range without interbreeding — see analysis of Wakefield (1958). *M. melanops* is apparently a secondary invader of southern Victoria.

(b) Morphologically Differentiated Isolates

The following are examples of geographically representative species, i.e., isolates that are so distinctive that they must now be genetic species:

(i) *Anthochaera paradoxa* (Tasmania). Parental stock: *A. carunculata* inhabiting the sclerophyll forests of southern Australia.

(ii) *Meliphaga flavicollis* (Tasmania). Parental stock: *M. leucotis*, inhabiting sclerophyll and mallee in southern Australia.

(iii) *Melithreptus affinis* (Tasmania). Parental stock: *M. lunatus* of the sclerophyll forests of southern Australia.

(iv) *Melithreptus validirostris* (Tasmania). Parental stock: *M. gularis*, inhabiting savannah woodland and dry sclerophyll in southern Australia. This form is somewhat less distinctive than the others and is probably not specifically distinct.

(v) *Acanthorhynchus superciliosus* (sclerophyll forests of southwest corner). Parental stock: *A. tenuirostris* of southeastern and eastern sclerophyll forests.

(vi) *Meliphaga notata* (rain forests of northeastern Australia). Parental stock: *M. analoga* of New Guinea (see previous discussion).

(vii) *Meliphaga macleayana* (Cairns-Atherton rain forests). Parental stock: *M. chrysotis* of New Guinea, now secondarily established in the rain forests of Cape York.

The total number of morphologically differentiated isolates in the Australian Meliphagidae will be seen in Table 3. These, if geographically representative species are excluded, total 18, and occur in 12 species, as follows:

Melithreptus lunatus, sclerophyll forest, 1, well differentiated; *Myzomela erythrocephala*, rain forest and mangroves, 1, major form; *M. obscura*, rain forest and mangroves, 1, minor form; *Acanthorhynchus tenuirostris*, sclerophyll forest, 2, minor forms; *Meliphaga notata*, rain forest, 1, minor; *M. gracilis*, rain forest, 1, minor; *M. flavescens*, tropical savannah woodland, 2, both minor; *Phylidonyris pyrrhoptera*, sclerophyll, 2, both minor; *P. novae-hollandiae*, sclerophyll, 1, minor; *P. niger*, sclerophyll, 1, minor; *Anthochaera chrysoptera*, sclerophyll, 2, one major, one minor; *A. carunculata*, sclerophyll, 1, minor; *Entomyzon cyanotis*, savannah woodland, 1, minor; *Philemon novae-guineae*, savannah woodland and mangroves, 1, minor.

Some 23 honeyeater species do not vary geographically in size or colour. Some 14 of these, however, are either insular species or have ranges so restricted that this would not be expected. About 5 are highly nomadic and several are partial nomads. *Melithreptus albogularis* has radiated outwards only fairly recently.

Speciation across Torres Strait has figured fairly prominently in the building up of the Australian honeyeater fauna though, proportionately, to a much less degree than in the Muscicapinae. *Philemon citreogularis* (Fig. 26), *P. corniculatus*, and *Meliphaga flavescens*, by contrast, are Australian savannah woodland species that have given rise to forms in southern New Guinea.

Hybrid zones do not occur in the Meliphagidae, though the relationships of the northern and southern forms in *Melithreptus gularis* merit investigation.

As noted, relatively few of the Australian Meliphagidae extend beyond the continent, but those that do tend to have morphologically differentiated insular isolates. Thus, *Myzomela dibapha* has about eight, mostly in the Celebes-Timor sector but with one on New Caledonia. *Lichmera indistincta* falls into many forms (over 5) in a range extending from Timor to the southwest Pacific. Other species have minor isolates in New Guinea.

Clines are common in the Meliphagidae, with most being demonstrations either of the Bergmann or Gloger effects. *Meliphaga lewini*, however, has a south-north cline of increasing bill length. The "plastic" interior species, *M. virescens,* provides examples of somewhat complicated colour variation. In *Melithreptus gularis* and *Meliphaga penicillata,* as in *Smicrornis brevirostris,* three colour forms extend in broad zones from east to west across the continent. As noted, they are associated with specific rainfall and temperature threshholds.

Family ZOSTEROPIDAE
(White-eyes)

Of three Australian species of *Zosterops, Zosterops lateralis* is equally well developed on the continent and in the southwest Pacific, and the other two (*Z. lutea* and *Z. chloris albiventris*) are derived from island species to the northwest of the continent.

Z. lateralis has an eastern and southern distribution in Australia and is essentially an inhabitant of sclerophyll forest and rain forest. *Z. lutea,* inhabiting the north and west, is a mangrove dweller. *Z. chloris albiventris* is confined to the islands off Cape York.

The species are sedentary except that *Z. lateralis* has a limited south-north migration in the southeast of the continent.

Speciation

Z. lateralis has morphologically differentiated isolates in southwestern Australia (*gouldi*) and on the Capricorn Islands off eastern Queensland and Lord Howe Island (*tephropleura*). The Tasmanian form (*tasmanica*), also occurring in southern Victoria, and that occupying the Murray Valley (*halmaturina*), apparently former isolates, are now connected with nominate *lateralis* (eastern New South Wales) by minor zones of intergradation. The Cairns-Atherton form (*vegeta*) may also be an isolate. *Zosterops lutea* has forms in the Hamersley and Kimberley segments that are probably isolates. There is clinal variation in both.

Z. lateralis tasmanica has invaded New Zealand and thence Norfolk Island, the Chathams, and Campbell Island, within recorded history. The species has some 6 morphologically differentiated isolates in the southwest Pacific.

The successive invasions of Lord Howe Island and Norfolk Island by members of the genus *Zosterops* provide some of the classic cases of speciation by multiple invasion. Whether or not these forms, however, came from a single point source is doubtful.

Family PLOCEIDAE
Subfamily ESTRILDINAE
(Finches)

Of the 18 species composing the Australian Estrildinae only two, and possibly three, are derived from outside of the continent. *Lonchura flaviprymna,* inhabiting a restricted area in the northwest, is an isolated derivative of *L. maja* of Indonesia, and *Erythrura trichroa* has recently colonized Cape York from New Guinea. *Lonchura castaneothorax* has a wide range in New Guinea (two morphologically differentiated isolates) as well as in Australia.

The seed-eating finches are mainly inhabitants of the dryer creekside thickets and savannahs of the north and east. *Zonaeginthus bellus-oculatus,* by contrast, is confined to thickets in the sclerophylls of the south, *Estrilda temporalis* to the sclerophyll and rain forests of the east, *Lonchura castaneothorax* to reedbeds and areas of rank grass (east and north), *Zonaeginthus pictus* to rocky outcrops in the central desert, and *Erythrura trichroa* to rain forest fringes in the northeast. Whilst none of the finches undertake regular seasonal movements, those inhabiting the central and northern regions are somewhat sensitive to shifts in the supply of seeds and surface water, bad seasons forcing groups to move to new areas.

Speciation

Zonaeginthus bellus is represented by a form in southwestern Australia so distinct that it can best be regarded as having reached species status (*oculatus*), whilst in the northwest and northeast of the continent, *Poephila acuticauda* and *P. cincta* are counterparts of each other (see figs. in Keast, 1958f).

Isolates that have reached a moderate or lesser degree of differentiation occur in *Poephila personata* and *Lonchura castaneothorax* (as between Arnhem Land and Cape York), in *Estrilda temporalis* (in Cape York and Mount Lofty Ranges), and in *Poephila phaeton*. In the last named, the black-breasted nominate form, occupying coastal northern Australia, but not Cape York, has given rise to a white-breasted isolate in New Guinea (*evangelinae*) which, in turn, has invaded Cape York to give rise to a derivative there (*albiventer*). This latter remains isolated.

Isolation without differentiation can be seen in the Tasmanian population of *Zonaeginthus bellus* and in the Australian population of *Erythrura trichroa*.

Hybrid zones occur in *Poephila bichenovii* and in *Poephila cincta*. In the former, the hybrid zone, between northwestern and eastern stocks, is in the general region of Alexandria to the west of the Gulf of Carpentaria (Fig. 2 in Keast, 1958f). In the latter, it occurs at the base of Cape York between a form that developed on the peninsula and an eastern Queensland one (Fig. 3, same paper).

Clinical variation occurs in many finch species. Of those that do not vary geographically (8) most have relatively restricted ranges. *Poephila guttata*, with an almost Australia-wide distribution, is an exception. It has, however, distinctive insular isolates on Timor and Sumba. *Erythrura trichroa* has 8 insular isolates beyond Australia.

The number of morphologically differentiated isolates in the Australian finches is 6 within the continent and 12 outside of it.

Family ORIOLIDAE
(Orioles)

Two genera occur in Australia: *Oriolus* (2 species) and the endemic Australo-Papuan *Sphecotheres* (2 species). The group is restricted to the savannahs (mainly) and sclerophyll and rain forests of the east and north. A certain amount of nomadism occurs in *Oriolus sagittatus*.

Speciation

O. sagittatus and possibly *O. flavocinctus* are divided into two recognisable stocks occupying the east and northwest of the continent, respectively. Both species, and *Sphecotheres vieilloti*, have isolates in southern New Guinea.

Family DICRURIDAE
(Drongos)

Only one member of this Palaearctic family reaches Australia. *Dicrurus bracteatus* does not vary geographically. It has about three morphologically differentiated isolates in New Guinea.

Family CRACTICIDAE
(Australian Butcherbirds and Magpies)

This small Australo-Papuan family is composed of 3 genera and 10 species. All are Australian except 2, which are confined to New Guinea. Three species are shared by New Guinea and Australia.

The cracticids, predators with body sizes ranging from that of a shrike up to that of a crow, include some of the most prominent elements of the Australian countryside, the magpies, currawongs, and butcherbirds. A generalized habitat, extending from sclerophyll forest to semi-arid country, is typical of *Gymnorhina* and most species of *Cracticus*. *Cracticus quoyi* and *Strepera graculina* are, however, restricted to mangroves and sclerophyll forest, respectively. *S. versicolor* has a southern peripheral distribution with sclerophyll forest, savannah woodland, and mallee being occupied.

None of the Cracticidae undertake seasonal movements other than those of a local nomadic nature.

Speciation

The amount of geographic variation in the Australian Cracticidae is great, especially in view of the relatively large body size. There are some 10-12 isolates of varying degrees of differentiation within the confines of the continent.

Tasmania has two isolates so distinct that they must be regarded as approaching, if they have not already reached, the status of genetic species: *Strepera* (*graculina*) *fuliginosa* and *S.* (*versicolor*) *arguta*. The southwestern isolate of the magpie, *Gymnorhina* (*hypoleuca*) *dorsalis*, is also generally recognised as having achieved that degree of morphological differentiation typical of a species. Lesser isolates occur in *Cracticus torquatus* (Tasmania), *C. quoyi* (eastern Cape York), *Gymnorhina tibicen* (2, one of Groote Eylandt and the other in the Macdonnell Range section of the continent), and in *G. hypoleuca* (Tasmania) (Amadon, 1951).

By far the most interesting species, from the viewpoint of differentiation in isolation, is *Strepera versicolor*. It has isolates in the Everard-Musgrave Ranges of central Australia (*centralia*), southwestern Australia (*plumbea*), and on Eyre Peninsula (*intermedia*), the last separated from the nearest relative (to the east) by a mere 20-mile wide water gap. Forms in southeastern South Australia (*melanoptera*) and in the Victorian mallee (*howei*) are now, apparently, secondarily connected with each other, and with the nominate form to the east, by minor hybrid zones.

Beyond the confines of the continent, *Gymnorhina tibicen* has a morphologically differentiated isolate in southern New Guinea, and *Strepera graculina* has one on Lord Howe Island.

Gracticus mentalis, possibly the most primitive member of its genus (Amadon, 1951), has presumably invaded Cape York from New Guinea where it now co-exists with *C. torquatus*. If this species is, in fact, its nearest relative this is the only demonstration of the final stage in the speciation process to be found in the Cracticidae.

Hybrid zones occur between the "species" *Gymnorhina hypoleuca* and *G. tibicen* in southern New South Wales-northern Victoria, and between the races of *Strepera versicolor* in eastern South Australia-western Victoria. It is probable, moreover, that the intergradation between forms within *Cracticus torquatus* and within *C. nigrogularis*, in the north and west of the continent, is also secondary. The hybrid zone between *Gymnorhina hypoleuca* and *G. tibicen*, extending as it does almost throughout the length of the Murray Valley (some 800 miles) requires proper study to determine whether or not it is stable or whether one form is extending at the expense of the other.

Colour and size clines occur in mostly widely ranging members of the Cracticidae within Australia (see Amadon, 1951).

Family GRALLINIDAE
(Mud-nest Builders)

The species composing the Australian mud-nest builders fall into three monotypic genera: *Grallina cyanoleuca*, *Struthidea cinerea*, and *Corcorax melanorhamphos*. A fourth member of the group, *Pomareopsis bruijni*, is confined to New Guinea.

Speciation

None of the Australian Grallinidae vary geographically.

Family PTILONORHYNCHIDAE
(Bower-birds)

The bower-birds are purely an Australo-Papuan group, with 6 species being confined to Australia, 9 to New Guinea, and 2 being shared.

The Australian species occupy a range of habitats from the dry interior to the eastern rain forests. The latter vegetation association is richest in species. Two species, the monotypic *Scenopoeetes dentirostris* and *Prionodura newtoniana*, are restricted to the highlands of the Atherton rain forest tract. There are no bower-birds in Tasmania.

Seasonal movements in the bower-birds are restricted to a local nomadism that has little effect on speciation trends.

Speciation

There are no instances of recently completed speciation in terms of range overlap by closely related species. All degrees of differentiation in isolation, however, occur (Mayr and Jennings, 1952). The rain forest species *Ptilonorhynchus violaceus* and *Ailuroedus crassirostris*, restricted to eastern Australia, each have distinctive southern and northern forms that are isolated from each other. The southern form of the latter is approaching that stage of differentiation typical of a species. In both cases the range gap is about 600 miles. Within the savannah grassland *Chlamydera maculata* there are eastern (*maculata*) and western (*guttata*) forms isolated by the general Simpson desert area along the eastern border of South Australia. These two are approaching, or have reached, that stage of differentiation typical of species. Here the range gap is apparently 400-500 miles. In *C. nuchalis* western and eastern forms are connected by a marked step in a cline (western

Queensland), indicating secondary intergradation between previously separated populations (Mayr and Jennings, 1952).

The savannah woodland *Chlamydera cerviniventris* extends to New Guinea without differentiation. The rain forest *Ailuroedus crassirostris*, however, has a range of racial forms in New Guinea.

Clinal variation occurs in the Australian bower-birds in *Sericulus chrysocephalus, Chlamydera maculata, C. cerviniventris*, and *C. nuchalis*.

VIII. THE MECHANISM OF SPECIATION ON THE AUSTRALIAN CONTINENT

The Nature of Geographic Variation in species. Quantitative Treatment

The nature of the variation in the 425 species constituting the sample is summarized on Table 3. Each species is graded according to whether it is monotypic or polytypic. The polytypic species are divided into those with clinal variation only and those with morphologically differentiated isolates, the number of the latter both within and beyond Australia (section to the east of Wallace's Line) being given. Where species are members of superspecies groups, this is stated. The isolates within Australia are subdivided into two groups: those with moderate to marked differentiations and those with slight differentiation. Finally, the number of hybrid zones (if any) is stated for each species.

The species sampled (425) are subdivisible as follows:—

Monotypic species:	188
Polytypic species with	
clinal variation only:	99
with isolates:	138
TOTAL: Polytypic species:	237

In terms of percentages then, it will be seen that 44 per cent of the species sampled (including those that are geographically representative) are monotypic, and 23 per cent have clinal variation only, whilst 33 per cent have isolates in Australia.

The number of morphologically differentiated isolates totals 213-220, averaging 0.5 per species for the fauna as a whole, and 1.6 per species for the 138 that have them. Of the isolates, 59 (27 per cent) have differentiated to a marked or moderate degree, and 154-161 (73 per cent) are but poorly differentiated.

Not included in the calculations are populations, particularly of sclerophyll forest species in Tasmania and the southwest, that are isolated but have not undergone any differentiation. The majority of these either have been isolated too short a time for differentiation to occur or are "conservative" species. Nevertheless, it should be recognised that such forms represent the first stage in the speciation process. Excluding these, it can be said that over 200 forms on the continent are potentially new species. One species, *Pachycephala pectoralis,* has 5 to 7 isolates.

Hybrid zones, indicating isolation that broke down before the differentiating stocks had reached specific level, occur in 30 species.

Examples of Species Formation and Intermediate Stages in the Speciation Process

The review demonstrates that active species formation is not only occurring today in most bird families but in almost every part of the continent. All speciation is spatial (geographic). There is no suggestion that it is occurring anywhere sympatrically (see Section XII).

Reference to Table 3 shows that the number of minor and major isolates in the Australian avifauna is large. Of even greater significance, however, in considering examples of intermediate stages in the speciation process are the many isolates that are now as, or more, different from their parental stocks than (genetically) proven species in their genera. These are the semi-species of Mayr (1942, p. 165). Finally, there are various instances of recently completed speciation, as demonstrated by marginal overlaps without interbreeding.

The families and subfamilies in which the full range of intermediate states in the speciation process occur within Australia are as follows: Accipitridae, Psittacidae, Menuridae, Campephagidae, Muscicapinae, Malurinae, Sittidae, Dicaeidae, Meliphagidae, Cracticidae. Possibly the Columbidae and Ploceidae also come into this category for *Geophaps scripta* and *G. smithi* in the former, and *Poephila acuticauda* and *P. cincta* in the latter, could actually be examples of the final stage in the speciation process, and not just unusually distinctive isolates. Those families that have Australian isolates at all stages of differentiation are: Ardeidae, Atrichornithidae, Timaliinae. In the Turnicidae, Alcedinidae, Silviinae, Zosteropidae, and Oriolidae, there are morphologically differentiated isolates of lesser degree.

Instances of Mayr's "proofs" of geographic speciation, i.e. the existence of superspecies, marginal overlaps, double invasions, and circle formation, occur in Australian birds as follows:—

(a) Superspecies

Almost one-third of Australian bird species belong to superspecies groups (column 6 in Table 4). Depending on the group, these lie mainly outside of, or within, the limits of the continent. In the long view, of course, several of the larger Australian birds are direct counterparts of species occurring in other parts of the world, e.g. the eagle *Aquila audax* is closely related to the Palaearctic Golden Eagle, *Aquila chrysaetos.* (Those species that belong to superspecies groups to the *west* of Wallace's Line have the figures in brackets.) Species belonging to superspecies centered in the island sector to the north of Australia and *east* of Wallace's Line include members of the families Columbidae (e.g., *Macropygia phasianella*), Psittacidae (*Trichoglossus moluccanus*), Alcedinidae (*Halcyon sancta* and *H. chloris*), Campephagidae (*Coracina tenuirostris*), Muscicapinae (*Arses kaupi, Monarcha melanopsis, Heteromyias cinereifrons*), Malurinae (*Gerygone* (*igata*) *richmondi*), Dicaeidae (*Dicaeum hirundinaceum*), Meliphagidae (*Myzomela dibapha, Meliphaga notata*), and Ploceidae (*Erythrura trichroa, Lonchura flaviprymna*).

Many superspecies groups are confined to the Australian continent. These include those in the following families and genera: Columbidae (*Geophaps*), Psittacidae (*Platycercus, Barnardius, Psephotus,* and *Neophema*), Muscicapinae (*Petroica*), Malurinae (*Gerygone, Sericornis, Amytornis, Stipiturus,* and *Malurus*), Sittidae (*Climacteris*), Dicaeidae (*Pardalotus*), Meliphagidae (*Melithreptus, Acanthorhynchus, Meliphaga, Anthochaera*), Ploceidae (*Zonaeginthus, Poephila*), and Cracticidae (*Gymnorhina, Strepera*).

(b) Marginal overlap of Recently Evolved Species

Some examples of this are as follows:—

Psittacidae: Neophema elegans, N. chrysostoma, and *N. chrysogaster*, overlap in parts of Victoria and South Australia. Areas of maximum concentration today suggest that *N. elegans* has arrived, secondarily, from the west, and *N. chrysogaster* from Tasmania.

Campephagidae: Coracina robustus and *C. papuensis* co-exist in the Cairns-Atherton area of Queensland, the latter presumably being the more recent arrival.

Muscicapinae: Petroica rosea and *P. rodinogaster* now breed together in southern Victoria. The latter developed in Tasmania.

Pachycephala rufogularis and *P. inornata* overlap in the mallee of Victoria, the latter apparently being a secondary invader from the west of the continent (Fig. 13).

Malurinae: Amytornis textilis and *A. modestus* both breed in the Macdonnell Ranges, the former having colonized the area from the west, and the latter from the east (Fig. 17a).

Hylacola cauta (western) and *H. pyrrhopygia* (eastern) now overlap distributionally in the Bendigo area of Victoria.

Sittidae: Climacteris picumnis (*melanota*) and *C. melanura* co-exist at the head of the Gulf of Carpentaria, the latter being an invader from the west (Fig. 22).

Dicaeidae: Pardalotus substriatus and *P. melanocephalus* live together in coastal eastern Queensland, the latter obviously being an invader from the north of the continent.

Meliphagidae: Melithreptus lunatus and *M. albogularis* occupy the same spatial relationship to each other as do *Pardalotus* but in this case the overlap zone extends for several hundred miles (Fig. 23). *Myzantha melanotis* and *M. flavigula* occupy adjacent zones in the Victorian mallee area, the former apparently being an "old" mallee form and the latter the recent invader.

Cracticidae: Cracticus torquatus and *C. mentalis* co-exist in Cape York, the latter possibly being a recent colonizer from New Guinea.

The co-existence of *Menura novae-hollandiae* and *M. alberti* in adjacent areas in northeastern New South Wales and southern Queensland is also an instance of range junction or overlap between related species though, in this case, obviously not a very recent one.

(c) Double Invasions

These, of course, are special cases of range overlap. They occur in two main areas: northern Australia, and Tasmania. There are also one or two apparent instances in southwestern Australia.

Entry into the Australian continent is only possible at a couple of points: through Cape York and, to a lesser degree, through the northwest corner. Tropical invaders can mostly only colonize down the coastal rain forest and monsoon forest tracts. This enables a fairly clear picture to be gained of the significance of double invasion in the speciation of Australian birds.

Colonization of northern Australia from the New Guinea-Timor segment:

(i) *Meliphaga lewini, M. notata,* and *M. gracilis* (honeyeaters). These three rain forest species now co-exist in the Cairns-Atherton area and represent successive waves of, and degrees of differentiation from, the ancestral stocks in New Guinea (Fig. 24).

(ii) *Philemon argenticeps* and *P. novaeguineae* (honeyeaters). In this case *P. argenticeps,* extending widely over the north of the continent, represents the first wave of colonization. Subsequent waves have independently entered Cape York (*P. novaeguineae yorki*) and Arnhem Land (*P. novaeguineae gordoni*) (Fig. 26).

(iii) *Coracina robusta* and *C. papuensis* (cuckoo-shrikes) are examples of an "old" Australian species (but whose ancestors must have entered from the tropics) being secondarily contacted, in the north of its range, by a later invader.

(iv) The two species of teal ducks (*Anas castanea* and *A. gibberifrons*), and the hovering kites (*Elanus scriptus* and *E. notatus*), represent somewhat older cases of speciation by double invasion. They now co-exist over a broad area.

(v) *Arses kaupi* and *A. telescophthalmus lorealis* (flycatchers) and *Meliphaga macleayi* and *M. chrysotis* (honeyeaters). In these cases the earlier and later arrivals, though isolated from each other in the Cairns-Atherton and Cape York sections, respectively, are so distinct that they must be genetic species.

(vi) Various infraspecific forms. "Simultaneous" invasion of Arnhem Land and Cape York by different races, which remain isolated in Australia, can be seen in *Butorides striatus, Myzomela erythrocephala,* and others. In a few cases a second wave of colonization by a stock, entering the continent at a common point, now hybridizes with the earlier one. In *Accipiter fasciatus* such hybridization occurs over a broad front. In a few species, the later invader has not yet contacted the earlier one. *Monarcha trivirgata* is an example of this, the New Guinea race occupying Cape York and the Australian one the country to the south of the Princess Charlotte Bay dry barrier, as in "(v)" above.

Colonization of Tasmania from Australia:

(i) *Acanthiza ewingi* and *A. pusilla* (Malurinae). In this case *A. ewingi* represents the derivatives of the earlier wave and *A. pusilla* (race *diemenensis*) the later one.

(ii) *Pardalotus quadragintus* and *P. punctatus* (Dicaeidae). This is a parallel case, with *P. quadragintus* the earlier element.

(iii) The two insular "species" of *Strepera* (*arguta* and *fuliginosa*) could represent a double invasion of the island by one or the other of the mainland species, i.e. either *S. versicolor* or *S. graculina.* Most workers feel, however, that a representative of each is involved.

Colonization of the sclerophyll forests of the southwest corner of the continent from the southeast:

Double invasion of the isolated pocket of sclerophyll forest in southwestern Australia by the robin genus *Eopsaltria* would appear to be the explanation for the occurrence there of two species, *E. georgiana* (representing the descendents of the earlier wave) and *E. australis* (*griseogularis*). Speciation in the *Malurus lamberti* complex could be accounted for by at least one of the species advancing from the east around the head of the Great Australian Bight.

(d) Speciation by Circle Formation

The only real instance of this in Australia is in the parrot *Platycercus elegans* (Fig. 11).

The honeyeater, *Meliphaga versicolor,* in that it developed its differences in New Guinea and from there has reinvaded Australia to occupy zones adjacent to its near relatives *M. virescens* and *M. fasciogularis,* presents, to a degree, a parallel in the north of the continent (Fig. 25). The white-breasted races of the finch, *Neochmia phaeton,* have had a similar origin.

Classificatory Position and Speciation

As will be seen from Table 4, summarizing the results in terms of families, there is a considerable amount of variation in the "speciation potential" of the different bird groups.

The hawks have only about 3 isolates in Australia and they are poorly differentiated ones. The larger water birds (grebes, herons and ducks) demonstrate similarly weak tendencies. In the case of the herons only 5 isolates are developed in Australia.

The ducks have no continental isolates though several occur in the Rallidae.

Large water birds have a very slow evolutionary rate, Howard (1946) having shown that many of them have not changed skeletally since the Miocene.

The pigeons (Columbidae), inhabiting a wide range of habitat types, have 10-11 isolates in Australia and, since they total 22 species, approximately reflect the average for the avifauna as a whole (0.5 isolates per species). The parrots (Psittacidae), equally diverse in habitat requirements, have 17-18 isolates in 33 species. Many of the species in this family, are, however, geographically representative. The ratio of isolates to species in the kingfishers (Alcedinidae) is 4 to 10.

In the cuckoo-shrikes (Campephagidae) there are 7 isolates in 8 species (1.0 per species). This is a figure typical of many of the small passerine groups, e.g. Malurinae with 61-62 isolates in 69 species, and the Muscicapinae with their 33-35 isolates in 43 species. The latter groups, it should be noted, are largely composed of sedentary species.

The Meliphagidae have 18 isolates in 67 species, although here again there are a number of geographically representative species. The Estrildinae, most of which are restricted to the north, have 6 isolates in 18 species. The Artamidae, which have continuous ranges and are nomadic, have no isolates in 6 species.

The endemic Australian Cracticidae, all of which are relatively large birds, have 11-12 isolates in 11 species. In this case, however, 4 of the latter are actually of uncertain genetic status so that the actual figure may be 1.5 isolates per species.

The family to which a species belongs can be seen to influence its potential for giving rise to new species not through any innate genetic characteristic so much as through what might be described as its ''ecological attributes.'' Included in these are body size and general mobility (large birds require a larger foraging area than small ones), nature of seasonal movements, type of food ''niche'' occupied, and habitat. Small insectivorous birds commonly live in a habitat that is specialized and restricted, and have poor dispersive capabilities.

The influence of the ''history'' of a group on speciation patterns is seen in the interesting differences between the flycatcher subfamilies Muscicapinae and Malurinae. The bulk of the genera in the latter are true endemics and speciation is taking place almost wholly *within* the continent. The Muscicapinae, however, whilst they do contain endemic genera, are best developed in the tropics and most of the isolation and speciation is taking place either outside of Australia or between New Guinea and Australia.

Habitat Specificity and Speciation

As noted, the majority of Australian bird species are restricted to, or reach the peak of their abundance, in one or another of the basic vegetation formations. Thus, as will be seen from Table 2, 16 per cent are rain forest dwellers, 16 per cent live in sclerophyll forest, 2 per cent in mallee, 4.5 per cent in mulga, 3 per cent in desert (spinifex) grassland, 3 per cent in mangroves, 14 per cent in swamps and marshes, and so on. The remainder are less specific but nevertheless are oriented to one or the other of the "intermediate-type" habitats of savannah woodland (28 per cent) and savannah grassland (11.5 per cent).

That the habitat category into which a species falls has an important influence on its potential for developing isolates and hence undergoing speciation will be seen from Tables 5 and 6. Thus the 70 rain forest species sampled have 31 morphologically differentiated isolates (0.5 per species). In addition to some recently developed geographically representative species (in Tasmania and southwestern Australia) the 80 sclerophyll forest species have 71-72 isolates (1.0 per species). The 113 savannah woodland species have 61-64 isolates (0.5 per species), the 44 savannah grassland species 10 isolates (0.2 per species). Ten mallee species have 4 isolates (0.4 per species). Fifteen mulga species have no isolates. Fifteen desert grassland (spinifex) species have 8 isolates (0.5 per species), 16 mangrove species, 10-11 (0.6 per species), and 54 swamp species only 11-12 (0.2 per species). The 9 species placed in the miscellaneous habitat category (e.g., *Lophophaps plumifera, Epthianura crocea*) have 7-8 isolates (0.8 per species).

If the figures be expressed as percentages (Table 6) it will be seen that of the total isolates about 14 per cent are rain forest forms, 33 per cent are sclerophyll forest birds, 30 per cent belong to savannah woodland, 5 per cent to savannah grassland, 2 per cent to mallee, nil to mulga, 4 per cent to desert grassland (spinifex), 5 per cent to mangroves, 5 per cent to swamps and marshes, and 3 per cent to miscellaneous habitats.

One of the significant facts revealed by Table 6 is that the bulk of the morphologically differentiated isolates or "incipient species" in Australia are coming from species that are predominantly inhabitants of sclerophyll forest and savannah woodland. These account for 33 per cent and 30 per cent, respectively, a total of 63 per cent of all isolates. In contrast with the tropical rain forest and mangrove habitats (that are mostly restricted to the northern fringe of the continent) these are "true Australian" vegetation formations. They have the combination of being extensive, biotically rich, and yet are broken up into several isolated tracts. In these regards they contrast with the dry-country vegetation formations, the savannah grassland, mulga, mallee, and spinifex, and with the swamp-river habitat.

The highest proportion of isolates that can be described as well differentiated, as compared to slightly differentiated, occur in savannah woodland (32 per cent), sclerophyll forest (25 per cent), and rain forest (22 per cent), respectively.

Hybrid zones are most numerous amongst the inhabitants of the savannah woodland, sclerophyll forest, and savannah grassland habitats, accounting for 54 per cent, 24 per cent, and 18 per cent of the figures, respectively. The savannah areas, occupying "intermediate" climatic zones are presumably the most sensitive and responsive to minor climatic shifts. Sclerophyll forest and savannah woodland have, more than any other associations, been subject to alteration by human settlement.

Species in which the only variation is of a clinal nature are most numerous in savannah woodland (43 per cent), sclerophyll forest (14 per cent), and savannah grassland (16 per cent).

Species that do not vary geographically are also most numerous in savannah woodland (many of the inhabitants of which are nomads, with others restricted either to the north or south), swamps (most inhabitants nomadic), rain forest (most are New Guinea immigrants restricted to the far north), and sclerophyll forest (many restricted to part of the southeast or Tasmania).

Species with isolates beyond Australia belong mainly to four habitat categories in Australia: mangroves, rain forest, sclerophyll forest and savannah woodland. In the case of the first two of these, this is to be expected as these vegetation formations have a wide distribution through the tropics. That so many sclerophyll and savannah woodland birds are involved might seem strange. The explanation is that the species concerned are those that already exhibit a fairly wide degree of habitat and ecological versatility in Australia, so that adjustment to a new habitat in the islands apparently presents no problem. Examples, and the number of isolates beyond Australia, are: the hawks (*Aviceda subcristata* (12), *Accipiter novaehollandiae* (19), *A. fasciatus* (6); the cuckoo-shrikes *Coracina papuensis* (9) and *C. tenuirostris* (18); the whistler *Pachycephala pectoralis* (51); the wood-swallow *Artamus leucorhynchus* (7); the dove *Geopelia striata* (3); the honeyeater *Philemon novaeguineae* (8); and the white-eye *Zosterops lateralis* (6). The rain forest *Rhipidura rufifrons*, by contrast, is an example of a species with a restricted habitat tolerance in Australia but that exhibits ecological versatility in the southwest Pacific where a number of diverse islands are occupied.

Seasonal Movements and Speciation

The influence of seasonal movements on isolation and speciation is summarized in Table 7. Two-thirds of the sedentary and migratory species vary geographically. Only one-quarter of the nomads, however, do so. Almost all of the isolates, as well as the hybrid zones, occur in the sedentary species. The number of morphologically differentiated isolates and the number of isolates per species for the three categories is as follows:

	Number of Morphologically differentiated isolates in Australia	Number of isolates per species
Sedentary species 294 (69%)	191-196	0.65
South-north migrants 32 (8%)	15-17	0.50
Nomads 99 (23%)	7	0.07

It will be seen that the nomadic way of life virtually eliminates any chance of isolation and speciation developing. This is brought out in equally striking fashion by the individual bird groups. The hawks and large water-birds are mostly nomads. Within the parrot family the nomadic *Melopsittacus* (Fig. 9) and *Leptolaimus* do not vary, whereas most genera composed of species that are essentially sedentary or resident, like *Psophotus* and *Platycercus*, have many isolates. Parallel cases are the nomadic *Certhionyx* and *Grantiella* amongst the honeyeaters, as compared to most members of *Meliphaga*. *Epthianura*, amongst the Malurinae, and *Artamus*, in the Artamidae have, on the one hand, sedentary species that show geographic variation and, on the other, nomadic species that do not show any at all.

South-north migration, by contrast, does not preclude the development of geographic variation and isolation, in part because many of these undertake seasonal movements over part of the range only, e.g. *Zosterops lateralis* and *Gerygone olivacea*. The relationship between variation and south-north migration in the campephagids *Coracina novaehollandiae* and *C. tenuirostris* has already been discussed. A reasonable inference with respect to most true south-north migrants in Australia is that, since they tend to inhabit the fertile coastal strip, they are able to return to the same areas to breed from year to year. This contrasts with the situation in nomads like *Epthianura tricolor* and *Lalage tricolor* which, though there is a south-north component to the movements, concentrate for breeding where seasonal conditions are maximal.

IX. GEOGRAPHIC ISOLATION

An understanding of the barriers initiating speciation in Australian birds necessitates a detailed review of the distribution of the major vegetation formations in the light of those bird species living in them.

Terrestrial Isolating Barriers

(a) Rain Forest

Rain forests are confined to the eastern seaboard and are broken up into a series of tracts and pockets (Fig. 5). There are, however, three main areas: (i) Cape York, (ii) Cairns-Atherton, (iii) and South Queensland-northern New South Wales. Each of these has some striking ornithological elements, the Cairns-Atherton section being particularly rich in this respect.

(i) *The Cape York rain forest tract:* These forests are chiefly of significance in that many New Guinea species have recently colonized the northern section. There are some 15 of these species, most undifferentiated: *Amaurornis olivaceus*, *Probosciger aterrimus*, *Larius roratus*, *Geoffroyus geoffroyi*, *Syma torotoro*, *Podargus ocellatus*, *Cacomantis castaneiventris*, *Drymodes superciliosus* (also on Roper River), *Microeca griseiceps*, *Tregellasia leucops*, *Monarcha frater*, *Sericornis beccarii*, *Craspedophora magnifica, Glycichaera fallax* and *Meliphaga chrysotis.* In several polytypic rain forest species the Cape York form represents a recent, independent wave of colonization from New Guinea, e.g. *Megaloprepia magnifica.*

The only species endemic to the Cape York rain forests is the honeyeater *Trichodere cockerelli.* There are, however, several distinctive races that have differentiated there, e.g. *Arses telescophthalmus lorealis.*

Ornithological data suggests that the Cape York rain forests have had the following history. They figured as "bridges" in earlier waves of colonization of the Cairns-Atherton forests by New Guinea species, but subsequently became reduced to such an extent that they could no longer support some of these forms. They have recently expanded again, but not to their former extent. The evidence for this is that a couple of genera, and species, requiring dense rain forest conditions, occur in New Guinea and in the Cairns-Atherton area, but not now in the intervening Cape York rain forests, e.g. the robin *Heteromyias,* the log-runner *Orthonyx* and, apparently, the swiftlet *Collocalia spodiopygia.* Again, the endemic bower-bird, *Prionodura newtoniana,* has New Guinea affinities. It is presumed that these forms became secondarily exterminated from the Cape York area. Tate (1952) finds similar distributional anomalies in the mammals of northeastern Australia, and feels too that these can only be explained in the above manner. An interesting alternative suggestion is, however, advanced. This is that, when Torres Strait was dry land and the climate was wetter, the confluence of the rivers flowing southwards from Papua must have approached that of the Australian ones flowing northwards across the Gulf of Carpentaria. The accompanying riverside forests would conceivably have provided a migration route from New Guinea to Atherton that by-passed Cape York.

As noted, there is currently much colonization of northern Cape York by New Guinea species suggesting re-establishment, or expansion, of this habitat.

(ii) *The Cairns-Atherton rain forests:* These are quite extensive and, in terms of the number of species endemic to them, are of considerable significance. There are some 8 such species· *Heteromyias cinereifrons, Colluricincla boweri, Arses kaupi, Oreoscopus gutturalis, Meliphaga frenata.* and *M. macleayana, Prionodura newtoniana* and *Scenopoeetes dentirostris* (both bower-birds). Some 25 rain forest and sclerophyll forest species have isolates of infraspecific rank here. They include *Acanthorhynchus tenuirostris, Ninox novae-seelandiae, Climacteris leucophaea, Eopsaltria capito, Pachycephala pectoralis, Gerygone (igata) richmondi, Acanthiza nana, Acanthiza pusilla,* and *Opopsitta diophthalma.*

There can be no doubt that the elevated and dissected Atherton area is a "refuge" of long standing. The rainfall today exceeds 80 inches per annum and in one small section reaches 160 inches per annum. It is probable that even in the event of a marked reduction in overall continental rainfall this sector would still be covered with rain forest.

(iii) *The southern rain forest tracts:* These extend from about the Bunya Mountains in southern Queensland to Dorrigo in central New South Wales. Thereafter they taper out as a series of small pockets. They are most dense and extensive in the Lamington area on the Queensland-New South Wales border.

Only between one-third and one-half of the true rain forest species extend south to this last sector. Within the 400-500 miles of the tract, moreover, there is a steady falling off in the number of species. A few, however, extend right through to the restricted, cold, subtemperate rain forests in the Dandenongs in Victoria, e.g. *Meliphaga lewini.*

Amongst the species endemic to the southern rain forests and associated wet sclerophylls are the bower-bird *Sericulus chrysocephalus,* the scrub-bird *Atrichornis rufescens* and the frogmouth *Podargus (ocellatus) plumiferus.* A lyrebird species, *Menura alberti,* is confined to the elevated Lamington segment in the north, where there is also a race of the southern sclerophyll whistler, *Pachycephala olivacea (macphersiona).*

(iv) *Barriers and Speciation:* Speciation occurs mainly between the three major tracts. The two commonest patterns are for the Cairns-Atherton and southern tracts to be occupied by distinctive isolates and for the Cape York and Cairns-Atherton tracts to be populated by forms that have reached a lesser degree of divergence. Examples are:—

Species with a distinctive isolate in each of the three main tracts: *Opopsitta diophthalma* (see Fig. 10), *Megaloprepia magnifica, Tregellasia capito-leucops.*

Species with distinctive isolates in the Cairns-Atherton and southern tracts only: *Ptilonorhynchus violaceus, Ailuroedus crassirostris, Sericornis citreogularis,* and *S. magnirostris. Gerygone* (*igata*) *richmondi* has, in addition, an isolate in the Bowen-Mackay tract.

Species with isolates in the Cape York and Cairns tracts only: *Machaerirhynchus flaviventer*, *Meliphaga analoga* and *M. gracilis*. In the flycatcher *Arses* the two tracts are populated by separate species. The warbler *Gerygone palpebrosa* has, in addition, a third isolate in the Mackay-Rockhampton section.

The barriers breaking up rain forest tracts in Australia, and hence the distribution of rain forest species, have been listed by Tate (1952). They are areas of dry savannah, as follows:—Coen-Cooktown gap (southern Cape York), width 150 miles; Burdekin gap (Townsville-Bowen), 125 miles; Mackay-Rockhampton gap, possibly less complete, about 150 miles; Rockhampton-Miriamvale gap (near Bundaberg), 100 miles; Toowoomba-Brisbane gap, 75 miles. A number of the bird species appear to be absent from the whole section between about Mount Spec, near Townsville, and the Bunya Mountains. In the case of these, the effective distributional barrier is some 400 miles wide. This is almost three times the distance between the Cairns-Atherton and Cape York tracts and explains the greater differentiation of many southern forms.

It is obvious that the distribution of rain forest bird species in Australia today can only be explained in terms of greater continuity of this habitat in the past. In particular, the "pockets" between the Cairns area and the Bunya Mountains must formerly have been larger and more extensive.

(b) Monsoon Forest

Monsoon forests or pseudo-rain forests form narrow strips along many of the coastal rivers in the dryer north and northwest of the continent, an area of summer monsoon rainfall Superficially, they resemble rain forests but differ in their restricted extent and relative dryness.

Monsoon forests, and the denser mangrove areas that are frequently adjacent to them, enable a number of eastern rain forest species to occur in the Northern Territory. There are about 12 of these and, with the exception of only two or three (e.g. *Chibia bracteata*, *Gerygone magnirostris*), all are represented by distinctive northwestern isolates. Such species are: *Rhipidura rufifrons*, *Piezorhynchus alecto*, *Drymodes superciliosa* and *Poecilodryas superciliosa*, *Lalage leucomela*, *Ptilinopus regina* and *Chalcophaps indica*, *Myzomela obscura* and *M. erythrocephala*.

Only a couple of species of birds are restricted to the monsoon forests of the Northern Territory. These species, *Gerygone chloronota* and *Ptilinopus* (*cincta*) *alligator*, have colonized the continent from western New Guinea and the Sumba Islands, respectively.

The barrier separating the Arnhem Land and eastern populations of rain forest species is the Gulf of Carpentaria and the dry country at its head, commonly leading to a range gap of 400-500 miles. The northwestern form of the rain forest flycatcher *Rhipidura rufifrons*, however, secondarily extends as far east as western Cape York.

(c) Sclerophyll Forest

The Australian sclerophyll forests are broken up into four sections, three of which are extensive (Fig. 5). These are: (i) The southeastern section extending from north of the Bunya Mountains to the southeastern corner of South Australia (about 1,300 miles), and typically bordered by the sea and Great Divide. (ii) Tasmania, insular, about 170 miles from north to south and slightly less from east to west, mostly sclerophyll. (iii) Southwest corner of the continent, a triangular section with a length of some 150 miles and a depth of 60 miles. (iv) The Mount Lofty Ranges and Kangaroo Island, two small, adjacent sections each measuring perhaps 100 by 20 miles.

In the east of the continent, various species that are basically sclerophyll inhabitants extend through the wetter coastal savannahs of eastern Queensland well beyond the limits of the sclerophyll forests proper. Again, in New South Wales, some extend a short distance inland through the denser riverside savannahs of the Murrumbidgee, Lachlan, and Murray, or into elevated sections to the west of the main range (Warrumbungle Mountains and Grampians).

The avifaunas of the four main sclerophyll areas may be summarized as follows:

(i) *Southeastern sector:* The main sclerophyll fauna is here. Almost all southwestern and Tasmanian sclerophyll forms have exact counterparts in the southeast, but the southeastern tract has various endemic forms absent from the others. The species restricted to the area include: *Menura novaehollandiae*, *Alectura lathami*, *Pycnoptilus floccosus*, *Cinclosoma punctatum*, *Callocephalon fimbriatum*, *Dacelo novaeguineae*, *Acanthiza lineata*, *Petroica rosea*, *Eurostopodus mysticalis*, *Meliphaga melanops*, *Manorina melanophrys.* The various nectar-feeding lorikeets, confined to the east, can equally be regarded as sclerophyll forest or savannah woodland forms.

(ii) *Southwest:* Two species only are unique to this area. These are the parrot *Purpureicephalus spurius*, whose nearest relative is believed to be a New Caledonian species, and the robin *Eopsaltria georgiana.* The latter probably represents the descendents of the first of two waves of colonization by the genus. Two wrens, *Malurus pulcherrimus* and *M. elegans,* are now known to be genetic species, though their counterparts in the east are infraspecific. An additional 10 forms, though isolated from their eastern relatives, are so distinct morphologically that they must have, or probably have, reached specific distinctness: *Calyptorhynchus baudini, Atrichornis clamosus, Sericornis maculatus* (extending into South Australia), *Malurus splendens, Neophema petrophyla, Platycercus icterotis, Climactoris rufa, Zonaeginthus oculatus, Gymnorhina dorsalis* and *Acanthorhynchus superciliosus.*

There are some 20 lesser isolates, most of them differentiated to only a minor extent. Perhaps 10 sclerophyll forest species have undifferentiated isolates in the southwest.

Southwestern Australia is remarkably rich floristically. For discussion of the flora, distribution maps of the various vegetation formations and factors delimiting them, see Gardner (1944; 1959).

(iii) *Tasmania:* The avifauna of this tract has a similar relationship to the continental southeast as does that of the southwest. There is one endemic genus, the monotypic *Acanthornis,* a small warbler-like bird. There are three proven genetic species: *Acanthiza ewingi, Pardalotus quadragintus,* and *Petroica rodinogaster. Lathamus discolor, Neophema chrysogaster,* and *Pardalotus striatus,* also occurring on the mainland, apparently originated in Tasmania. About 12 endemic Tasmanian forms are still isolated from their mainland relatives but exceed, or equal, the degree of differentiation typical of species: *Tribonyx mortieri, Platycercus caledonicus, Sericornis humilis, Petroica vittata, Meliphaga flavicollis, Anthochaera paradoxa, Melithreptus affinis, M.* (*gularis*) *validirostris, Strepera fuliginosa* and *S. arguta* (the last three the least distinct).

Twenty or so of the mainland sclerophyll species have isolates on Tasmania that have attained a slight to moderate degree of distinctness, whilst perhaps a dozen are represented by undifferentiated populations.

(iv) *Mount Lofty Ranges and Kangaroo Island:* This area is merely an outlyer of the southeastern tract. Various species do not, however, extend through to here.

In about 10 species, the populations isolated here have undergone a minor amount of differentiation, e.g. *Phylidonyris pyrrhoptera, P. novaehollandiae, Acanthorhynchus tenuirostris, Zosterops lateralis, Stipiturus malachurus, Acanthiza lineata, A. nana, A. pusilla, Strepera versicolor, Climacteris leucophaea.* Gene flow has been resumed with the east in *Zosterops lateralis* and *Pachycephala pectoralis,* presumably as a result of a minor amelioration in climatic conditions. In a few instances the Kangaroo Island populations have differentiated to a minor extent from the Mount Lofty ones (see Table 8).

(v) *Barriers and Speciation:* Variation and speciation in the sclerophyll forest species follow a clear-cut pattern. They are typically broken up into three to four stocks. In a couple of instances there are differentiated populations in each of the tracts, e.g. *Acanthorhynchus tenuirostris, Zosterops lateralis.* The important trends, however, occur between Tasmania, the southwest, and southeast.

Species with distinctive isolates both in Tasmania and in the southwest: *Gymnorhina tibicen* supersp., *Platycercus eximius* supersp., *Anthochaera carunculata* supersp., *Rhipidura fuliginosa, Melithreptus lunatus* supersp., *Phylidonyris novae-hollandiae, Pardalotus punctatus* supersp., *Acanthiza pusilla, Sericornis frontalis* supersp., *Strepera versicolor., Malurus cyaneus-splendens* group, *Calamanthus fuliginosus, Stipiturus malachurus, Pachycephala pectoralis, Turnix varia.*

Species with distinctive isolates in the southwest only, i.e. in which the Tasmanian stock (when present) has not differentiated: *Zonaeginthus bellus, Petroica multicolor.* The following do not occur in Tasmania: *Eopsaltria australis, Phylidonyris niger, Dasyornis brachypterus* and *D. broadbenti.*

Species in which the Tasmanian stock alone has differentiated: *Phylidonyris pyrrhoptera, Platycercus elegans* supersp., neither of which occur in the southwest; *Meliphaga leucotis* supersp; *Aquila audax,* with a wide range over Australia, has a minor form in Tasmania.

The four sections are isolated from each other by the following barriers:—

Bass Strait. This has a width of 100 miles but intervening islands reduce the maximum water gap to 50 miles.

Coorong arid tract, southeastern South Australia. This 90-100 mile wide section of sand and sparse scrub isolates the Mount Lofty Ranges.

Spencer Gulf. This deep coastal indentation is some 50 miles wide at the mouth.

Nullarbor Plain and the Great Australian Bight. A vast tract of sparse and stunted desert vegetation, 500 miles wide, stretches westwards from Eyre Peninsula. It is this and Spencer Gulf that isolate the sclerophyll forest of the southwest corner. (see also page 439.)

There can be no doubt that the sclerophyll forests of southeastern and southwestern Australia must at one time have extended much closer to each other, or else that a tongue of "damp scrub" suitable as a bird habitat, joined them. Isolation resulted from, in all probability, post-Pleistocene climatic and sea-level changes. To what extent the arid Nullarbor barrier would have to be narrowed to permit an interchange of sclerophyll birds between east and west cannot be stated. Some species are better adapted to dry conditions than others, as seen from the varying distances between eastern and western populations in different species (note Fig. 6 in Serventy and Whittell, 1951). On the other hand, the 90-100 mile wide Coorong arid barrier is completely effective in a large number of species.

It is interesting to note that a couple of the sclerophyll forest species that occur both in the east and the southwest are absent from the Mount Lofty-Kangaroo Island section, e.g. *Eopsaltria australis*, *Phylidonyris niger*, despite the occurrence of suitable habitat. This suggests that there has been secondary extinction in the region. On the other hand, a couple of southwestern forms have secondarily crossed the Nullabor Plain to occur in the savannah woodlands of Eyre Peninsula.

(d) Savannah Woodland

Whilst many savannah woodland species occur throughout the range of the association there are distinct northwestern and southeastern components. The former is richer. These could be said to inhabit the "tropical" and "temperate" section of the woodlands, respectively, although no real dividing line exists between them.

The vegetation maps show savannah woodland as extending in a broad belt through the eastern and northern sections of the continent (Fig. 5) but bird studies demonstrate that there is a major severance of the fauna into northwestern (Arnhem Land) and eastern components. There is, in addition, a minor differentiation in the case of a few species as between Cape York and the woodlands farther south. An extensive tract of country in the Hamersley section of Western Australia, shown on the map as savannah grassland but containing various (predominently) savannah woodland bird species, and the isolated desert mountain ranges of central Australia, can also best be considered here. Melville Island, lying some 20 miles off Arnhem Land, has a few minor isolates. The restricted section of savannah woodland in southwestern Australia is of no significance ornithologically.

(i) *Kimberleys and coastal Northern Territory:* This tract contains many endemic elements, whilst others characteristic of the northern coastal fringe as a whole obviously originated here. Northwestern species without counterparts in the northeast include the rock pigeons *Petrophassa albipennis* and *P. rufipennis*, the finches *Lonchura pectoralis* and *L. flaviprymna*, and the honeyeater *Meliphaga albilineata*. Northwestern species with counterparts in the northeast are listed below.

(ii) *Cape York and northeastern Australia:* This section is populated by virtually the same species, or their counterparts, as the previous one. In a few instances, however, it has been invaded by additional savannah species from New Guinea, e.g. the friarbird *Philemon novaeguineae* (*yorki*) and the white breasted race (*albiventer*) of the finch *Poephila phaeton*.

Speciation is actively occurring as between the northwest and northeast of the continent in savannah woodland birds:

Northeastern Form	Northwestern Counterpart
Proven Species (contact without interbreeding)	
Climacteris picumnus melanota	*Climacteris melanura*
Isolated forms that have obviously reached that stage of differentiation typical of species.	
Geophaps smithii	*Geophaps scripta*
Platycercus adscitus	*Platycercus venustus*
Poephila cincta	*Poephila acuticauda*
Malurus dulcei	*Malurus amabilis*
Well differentiated isolates	
Psephotus c. chrysopterygius	*P. c. dissimilis*
Poephila personata leucotis	*Poephila p. belcheri*
Lesser Isolates	
Entomyzon c. cyanotis and *E. c. hedleyi*	*Entomyzon cyanotis albipennis*
Halcyon m. macleayi	*Halcyon m. publa*
Neositta chrysoptera leucocephala and *N. c. striata*	*Neositta chrysoptera leucoptera*
Myzomela erythrocephala kempi	*Myzomela erythrocephala*

In addition to the above, it is probable that the honeyeater *Melithreptus albogularis*, and possibly *Pardalotus melanocephalus*, developed in northwestern Australia and are secondary inhabitants of eastern Australia (Fig. 23).

(iii) *Eastern Australia:* Included in the savannah woodland inhabitants restricted to (south) eastern Australia are *Pedionomus torquatus* (plain wanderer), the honeyeaters *Meliphaga fusca* and *Plectorhyncha lanceolata,* and the finches *Lonchura modesta* and *Zonaeginthus guttatus.* Most of these are distributed north to about 18 or 20-degree line of latitude, i.e. they do not occur on Cape York.

Evidence of the (former) severance of Cape York and southeastern savannah woodland species is seen from the existence of distinct northern and southern forms in the tree-creeper *C. picumnus melanota* and *C. p. picumnus* (Fig. 22), the flycatcher *Seisura inquieta* (Fig. 15), and the kingfisher *Dacelo novaeguineae*. In these species the two forms are apparently still isolated. The finch *Poephila cincta*, however, has a hybrid zone at the base of Cape York.

(iv) *Hamersley section of midwestern Australia:* A number of species have distinctive isolates in this section. Amongst these are *Coracina novaehollandiae*, *Pomatostomus temporalis*, *Dacelo leachii*, *Geopelia striata*, *G. humeralis*, *Ocyphaps lophotes*, now with a somewhat expanded range, and *Climacteris melanura*. *Lophophaps plumifera* has a distinctive form (*ferruginea*) amongst the rocky outcrops of the area.

The range of typical savannah woodland forms in this section (*Climacteris melanura wellsi*) will be seen in Figure 22.

(v) *The mountains of central Australia:* The desert mountains constitute a refuge and relict area for some plant and some invertebrate species, populations of which are isolated there hundreds of miles away from their nearest relatives on the coast (Keast, 1959d). Their existence is interesting evidence of a formerly higher rainfall in central Australia. At the vertebrate level, the desert mountains are chiefly of significance in permitting a number of species to live in the interior of the continent that would otherwise be unable to do so.

Two savannah bird species have distinct isolates in the central mountains: *Rhipidura fuliginosa*, in the Levi Range, and *Strepera versicolor*, in the Everard Range.

(vi) *Melville Island:* Some 6-8 Arnhem Land forms have minor isolates on this island (see Table 8).

(vii) *Barriers:* There can be no doubt that the barrier isolating northwestern and eastern savannah woodland components is the tongue of dry country extending through the centre of the continent to the head of the Gulf of Carpentaria. The 30-inch rainfall isohyet reaches the sea here (Fig. 4). A better appreciation can, however, be gained from the climatological map (Fig. 4a), humid and sub-humid zones being isolated by an extensive tract of semi-arid country. A minor fall in sea-level would materially reduce the size of the Gulf.

Differentiation as between Cape York and eastern savannah woodland species has probably taken place on either side of the tongue of dry country (shown on rainfall but not vegetation maps) extending through to the sea in the general Townsville-Burdekin River area (Fig. 4). This was probably more effective previously.

The barrier cutting off the Hamersley section from the north is the tract of the Great Sandy Desert that reaches the sea in northwestern Australia in the vicinity of Eighty Mile Beach, a barrier perhaps 80-100 miles wide. Another arid tract, covered mainly by mulga scrub, extends through to the sea in the general vicinity of Shark Bay. Though vegetated, this effectively keeps the advance elements of southwardly-colonizing savannah and grassland species of the Kimberleys from reaching southwestern Australia.

The mountains of central Australia are surrounded by extensive tracts of arid sand-plain desert.

(e) Savannah Grassland

The ground-feeding grassland species and aerial feeders that require flat plain with scattered trees for perching are either confined to this habitat or reach their peak of abundance here. These include several quail species, the chats *Epthianura tricolor* and *E. aurifrons* (the latter mainly an inhabitant of saltbush within the savannah), a couple of species of *Malurus*, and the cuckoo-shrike *Pteropodocys maximus*.

Savannah grasslands cover extensive areas of Australia. Their borders are sometimes poorly defined, there is interdigitation with other associations and, within the area defined as grassland on the map, there are enclosed tracts and areas of savannah woodland, mulga and saltbush. Their continuous nature and the fact that a high proportion of the avifauna is nomadic explains the virtual absence of isolation and speciation in the bird inhabitants of this habitat.

Barriers: Nil.

(f) Mulga

Many bird species inhabit mulga and adjacent associations (especially savannah grassland) to an equal degree. Only a few species are confined to mulga so that the habitat is of limited significance ornithologically. These include, however, the honeyeater *Conopophila whitei* and the tree-creeper *Climacteris affinis*.

The mulga tracts are continuous, or are made continuous by interdigitation of the dry-country vegetation formations. The small number of plant species composing them and their semi-arid to arid nature necessitate a certain amount of nomadism in their avian inhabitants. Neither isolation nor speciation are to be found in mulga birds.

Barriers: Nil.

(g) Mallee

The mallee extends across southern Australia as a broad, discontinuous belt. The main eastern and western sections, perhaps 700 and 500 miles long, are separated by a gap of some 200 miles. Such differentiation as is occurring in the 10-12 true mallee species (as distinct from those also inhabiting other habitats) occurs between these sections. In *Leipoa ocellata, Drymodes brunneopygia,* and *Pardalotus xanthogpygus* there is no differentiation. It is slight in *Pachycephala inornata, Cinclosoma castanotum, Psophodes nigrogularis, Glossopsitta porphyrocephala,* and marked in *Stipiturus malachurus.* In *Myzantha* the eastern mallee form has now reached species status (*M. melanotis*). In the genus *Pachycephala* there is no doubt that the eastern species *P. rufogularis* also originated and developed in that section. *Amytornis striata* and *Calamanthus* (*fuliginosus*) *campestris,* ranging widely through the arid country of the western half of the continent, have distinctive isolates in the southeastern mallee.

The distribution of mallee is associated with special edaphic, as well as rainfall, factors. The gap at the head of the Great Australian Bight (Nullarbor Plain) is due to edaphic, as well as rainfall, factors. Mallee occurs only on alkaline (limy) sands and is absent from stony lateritic areas.

(h) Desert (Spinifex) Grassland

(i) Stony (Gibber) Desert

Arid sand-desert, with its large clumps of *Triodia* or porcupine grass, provides a limited but specialized habitat for several bird species, especially members of the genera *Amytornis* and *Malurus,* and *Stipiturus ruficeps.* The bare gibber deserts are the homes of *Ashbyia lovensis, Aphelocephala pectoralis,* and *Cinclosoma cinnamomum.* The two groups are differently adapted, dense cover being just as important to the former as it is unimportant to the latter.

The spinifex association is somewhat broken up by salt lakes, gibber desert, and tracts of mulga. Only in *Amytornis*, however, do morphologically differentiated isolates occur.

(j) Mangroves

Whilst mangroves extend discontinuously right around the Australian coastline, only in the northern two-thirds do specialized mangrove bird species occur.

In contrast with the other vegetation formations little precise information is available in the distribution of, and gaps in, the mangrove forests. Much isolation and speciation is taking place in mangrove bird species, however.

Distinctive bird forms occur in the following areas: (i) Shark Bay (*Butorides striatus, Zosterops lutea* (barely distinguishable), *Pachycephala lanioides*); (ii) Midwestern Australia, especially the Ashburton and Point Cloates sections (*Pachycephala pectoralis, P. lanioides, Gerygone* (*magnirostris*) *tenebrosa;* (iii) Derby-Fitzroy River area (*Pachycephala pectoralis*) or Derby-Kimberley area generally (*Zosterops lutea, Butorides striatus, Gerygone laevigaster*); (iv) Northern Territory-Arnhem Land (*Pachycephala simplex, Zosterops lutea, Gerygone laevigaster, Butorides striatus, Pachycephala lanioides, Cracticus quoyi;* (v) Northeastern Queensland (*Pachycephala simplex, Butorides striatus, Cracticus quoyi*); (vi) Eastern and southeastern Queensland. The species *Meliphaga fasciogularis* and *Gerygone cantator* are confined to this last sector.

The mangrove heron, *Butorides striatus*, has the maximum number of morphological forms amongst the mangrove species. The distribution of these forms corresponds generally to those in other mangrove species, as shown in Figure 8.

Known gaps in mangrove distribution include the arid Eighty Mile Beach section and stretches of rocky and sandy coastline along the north (see Vegetation Region map in Atlas of Australian Resources). In addition the mangrove forests themselves vary in nature from place to place, some being sparse and open, others relatively damp and luxurious. They are best developed in inlets and along the lower stretches of rivers.

(k) Swamps, Marshes and Streams

This habitat, covering only an insignificant area of the continent and being best developed in the southeast, has a rich and specialized avifauna. Most water-birds wander widely, however.

A few species have morphologically differentiated isolates in southwestern Australia and/or Tasmania, e.g. *Megalurus gramineus, Porphyrio porphyrio.* The barriers are the arid Nullarbor Plain and Bass Strait.

(l) Miscellaneous Habitats

The pigeons *Lophophaps plumifera* and *Petrophassa albipennis-rufipennis,* requiring rocky outcrops, are broken up into morphologically differentiated isolates by tracts of country lacking in, or having only small areas of, this habitat. Sandplains and sand-hills, the bulk of which would probably stem from the onset of aridity at the end of the Pleistocene, are important in limiting distribution. The northern species of *Amytornis* are confined to three rugged river systems where broken rock and spinifex or undergrowth occur in combination. In these and other species the distributional barriers are tracts of country deficient in permanent cover.

(m) Bird Species ranging through many Vegetation Formations

There are no barriers to distribution in the case of these species.

Water as an Isolating Barrier

(a) Speciation between Australia and New Guinea

As noted in Section IV (2) the width of Torres Strait is some 100 miles, with the longest water crossing perhaps 70 miles. Its maximum depth in the section immediately to the north of Cape York is only 30 feet. The Strait was dry during part of the Tertiary and on two occasions during the Pleistocene.

An assessment of the importance of Torres Strait as a distributional barrier is greatly complicated by the climatic and vegetation differences between the land-masses on either side of it. The north of Australia is relatively dry, is covered by savannah woodland, and is populated by bird species adapted for this kind of life. New Guinea species, by contrast, are largely inhabitants of tropical rain forest and montane forest. There is only a small endemic savannah woodland element.

For the greater part New Guinea has contributed rain forest genera and species, and a few mangrove species, to the Australian avifauna (see Section IX (a)). Australia is mostly supplying savannah woodland species to the restricted areas of that habitat in southern New Guinea.

At the present time Australia and New Guinea have about 191 species of land and fresh water birds in common. These could be allocated, in terms of origin, as follows:

Species of Australian origin,	about 92
Species of New Guinea origin,	about 66
Origin doubtful	about 33

Of these, perhaps 52 of the Australian species (about 58 per cent) have undergone differentiation in New Guinea and some 53 of the New Guinea species (78 per cent) have undergone differentiation in Australia. The smaller percentage figure in the former case is because large water birds (wanderers) and hawks are prominent in the list.

Apart from currently occurring speciation between the two land masses, it is obvious that many bird groups today are represented by equivalent genera and species in the two areas, demonstrating that the interchange has gone on over a considerable period of time. This is particularly marked in the larger families like the honeyeaters and flycatchers but is seen in the smaller groups as well. Thus, for example, the subfamily Grallinae (Grallinidae) has the monotypic genus *Grallina* in Australia and the monotypic *Pomareopsis* in New Guinea, and a parallel situation, in the Timaliinae, is suggested by *Psophodes* and *Androphobus*. Some of the larger Australo-Papuan genera like *Meliphaga* (Meliphagidae), *Pachycephala* and *Gerygone* (Muscicapidae) have a series of equivalent species in the two land masses.

(b) Speciation between Australia and the Near Offshore Islands

Islands are few in number off the Australian coast. Tasmania alone is a large island capable of supporting a moderate-sized differentiating avifauna. Three of the smaller offshore islands have several minor races: King Island in Bass Strait, Kangaroo Island off southeastern South Australia, and Melville Island off Arnhem Land.

The Australian offshore islands on which differentiating forms occur, their distance from the mainland, and the names of the forms are listed in Table 8.

The total number of morphologically differentiated isolates on the offshore islands (including semi-species but excluding cases of speciation by double invasion) is 63. This figure represents about 34 per cent of the total, a somewhat high figure.

Almost all of these, however, are on Tasmania.

(e) Speciation between Australia and the More Remote Islands

The position of the major islands and their distances from the Australian continent are discussed in Section (IV) and are shown in Figure 2. Their avifaunal relationships with Australia are summarized in Table 9.

Apart from New Guinea, it will be seen that a significant two-way faunal interchange has only occurred between Australia and Timor. This island, moreover, lies on a main immigration route from Indonesia to Australia, and vice versa.

Australia has supplied species to New Caledonia, Lord Howe Island, and New Zealand, over a period, but there is no indication of the continent having received new land and freshwater bird species from these sources.

The avifaunal relationships between the more remote islands and Australia may be summarized as follows:

Timor: The breeding land and freshwater avifauna of this island possibly totals 130 species, to which various chance visitors must be added. Oriental and endemic elements are pronounced, though repeated interchange with Australia has occurred. Mayr (1944b) lists 22 bird species that have obviously entered Australia from Timor and points out that Australia has contributed a least 17 species to the avifauna of the island.

New Caledonia: The land and freshwater avifauna totals 68 species, out of which about 18 species are colonizers from Australia. The island has a monotypic family, the Kagu (Rhynochetidae).

Several of the Australian colonists have reached, or passed, that stage of morphological differentiation typical of genetic species. These include a robin (*Eopsaltria flaviventris*), a cuckoo-shrike (*Coracina caledonica*), and an owlet-nightjar (*Aegotheles savesi*). The endemic populations of the bustard-quail (*Turnix varia*), the nightjar (*Eurostopodus mysticalis*), a honeyeater (*Myzomela dibapha*), and others, are racially distinct. There are no apparent instances of "speciation by double invasion."

Lord Howe Island: The avifauna of this island is drawn from New Caledonia and the other islands to the north, New Zealand, and Australia. Several of the European species occurring on the island are self-introduced from New Zealand. The genus *Zosterops* has invaded the island twice though whether or not this has been from a single point source is uncertain.

Of the 20 or more species of land and freshwater birds breeding on Lord Howe Island some 5 are of Australian origin. Of these the fantail *Rhipidura cervina* is now fairly distinct, the cracticid *Strepera graculina* (*crissalis*) and the white-eye *Zosterops lateralis* (*tephropleura*) somewhat less so.

New Zealand: The breeding land and freshwater avifauna amounts to some 80 species, plus over 20 "stragglers" that occasionally arrive from Australia.

Several unique families of birds are confined to New Zealand: the kiwis (Apterygidae), extinct moas (Dinornithidae and Anomalopterigidae), bush wrens (Xenicidae), wattled crows (Callaeidae), as well as aberrant genera like *Nestor* and *Strigops* (parrots).

Australia has had an important influence on the development of the avifauna, with colonization proceeding over a considerable period of time. Some of these colonizers are now generically, others specifically, or racially, distinct. The Meliphagidae are represented by a couple of endemic genera in New Zealand. In the case of the robin-like flycatchers one genus is endemic (*Miro*) and the other (the Australian *Petroica*) has given rise to a species (*P. macrocephala*) in the islands. The stilts *Himantopus novaezealandiae* and *P. leucocephalus* (race *albus*) represent a case of speciation by double invasion. The flycatcher *Rhipidura fuliginosa* has only differentiated to the race level (*fuliginosa*), as has the kingfisher *Halcyon sanctus* (*vagens*). In more recent times an additional 8 to 10 Australian species have colonized New Zealand (see list in Falla (1953)) and now breed there. The latest of these is the swallow *Hirundo neoxena*, which became a breeding species in 1958. These forms have yet to differentiate in the new environment.

(d) Radiation of Australian Species in the Archipelagos of the Southwest Pacific

Many bird species that are obviously of Australian origin, or that can reasonably be inferred to be such, are represented by a series of insular isolates in the southwest Pacific area. These are discussed in Section XIII. They include *Accipiter novae-hollandiae*, *Nycticorax caledonicus*, *Dupetor flavicollis*, and *Petroica multicolor* (Table 9). In some cases the initial range extension would appear to have taken place through New Guinea but in others it has apparently been by way of New Caledonia.

X. HYBRID ZONES AND STEPPED CLINES—EVIDENCES OF FORMER ISOLATION

Hybrid zones and stepped clines occur in many bird species and in various parts of the Australian continent. They are not, however, common (see Table 3). Hybridization in Australia has not yet been subjected to a proper study. This will be necessary before the relative status of *Gymnorhina tibicen* and *G. leuconota*, *Barnardius zonarius* and *B. barnardi*, *Sericornis maculatus* and *S. frontalis*, *Platycercus eximius* and *P. adscitus*, can be determined.

Hybrid Zones

Some of the more common cases of hybridization and the circumstances surrounding them are as follows:

(i) *Northwestern Australia:* Hybridization occurs between the Hamersley and Kimberley races of *Dacelo leachii*, *Coracina novaehollandiae*, and *Geopelia humeralis* to the north of the Eighty Mile Beach arid barrier, some individuals of the southern forms having managed to bridge it. The Hamersley population of *Ocyphaps lophotes* intergrades both with its counterparts in the Kimberleys and in central Australia, indicating a generalized range extension in this species.

(ii) *Northern Territory:* The northwestern and eastern races of *Poephila bichenovii* hybridize in the general region of Alexandria Downs, N.T. (map in Keast, 1958f), the result of the eastern race having secondarily extended its range westward across the dry country at the head of the Gulf of Carpentaria.

(iii) *Base of Cape York:* Two races of the finch *Poephila cincta* hybridize in this area. One obviously developed on Cape York and the other in eastern Queensland. Contact is the result of both having extended their ranges outwards into the dryer intermediate country.

(iv) *Tip of Cape York:* The small water-kingfisher *Alcyone pusilla* has a variable population here, apparently due to the intrusion of genes from either the northwestern or New Guinea race, or both.

(v) *Darling Downs and northeastern New South Wales:* There is occasional hybridization between the parrots *Platycercus eximius* and *P. adscitus* in this region. It is not clear which of the above has invaded the range of the other but the one obviously developed in the southeast and the other in the northeast of the continent, respectively. (Fig. 12)

Intergradation between the three eastern races of *Malurus lamberti* occurs in this sector.

(vi) *Southern New South Wales and northern Victoria:* In the genus *Gymnorhina,* a white-backed form occupies the southern parts of the continent (*leuconota*), and a black-backed one (*tibicen*) inhabits New South Wales and Queensland. A hybrid zone, corresponding generally to the Murray Valley but in places swinging 50-100 miles to the north, or south, of it connects the two forms today. The zone of hybridization is perhaps 800 miles long. The habitat of *Gymnorhina* is open grassland with scattered trees, a form of association that has vastly increased as a result of clearing of the country.

The possibility that there may be a broad hybrid zone in the striped-crowned pardolates (Dicaeidae) in this section of the continent, with *Pardalotus ornatus* itself being a hybrid form, has already been discussed.

(vii) *Southeastern South Australia: Platycercus elegans* has a series of distinctive intermediate populations in this section connecting the typical form (on Kangaroo Island) with *flaveolus* in the Murray Valley. Cain (1955) suggests that these forms, and *flaveolus* itself, represent former isolates that developed in forested pockets during a more arid phase and that hybridization is the result of secondary range extension.

Further instances of hybridization in South Australia occur as a result of the eastward spread of *Barnardius zonarius* and *Sericornis maculatus,* these meeting their counterparts (*B. barnardi* and *S. frontalis*) in the Flinders Range and Cape Jervis-Mount Lofty sections, respectively. It is not known whether hybrids are rare or common.

(viii) *Complicated Continent-wide Hybridization Patterns: Neositta chrysoptera superspecies:* This case, studied by Mayr (1950b) is illustrated in Figure 21. Mayr has recorded intergradation between the southwestern and southeastern forms in western Victoria and between the southeastern and central Queensland forms in northeastern New South Wales. Thereafter, a series of somewhat transitional forms tend towards the Cape York one. The status of the northwestern counterpart is unknown since it is apparently still isolated from the northeastern ones. Here too, however, there has been considerable secondary range spread.

Neositta is of particular interest in several ways:

(a) The geographic counterparts had reached a significant degree of morphological difference, with many characters involved, before the barriers broke down or were abridged. (b) Hybridization has simultaneously occurred in many places. (c) In some cases hybrid zones are narrow, in others broad. (d) Many of the areas where hybrid zones and range extensions occur are paralleled in other groups. The two western forms, for example, reflect the generalized eastward expansion that is taking place in various northwestern and southwestern forms (Keast, 1956a).

Pachycephala pectoralis. This species, also analysed by Mayr (1954a), has a peripheral distribution, in the course of which it occupies a wide range of habitats. It has no fewer than 12 geographic races, 8 to 9 of which are apparently isolates. Minor hybrid zones connect the others which occur in the following areas: western Victoria, southern New South Wales, southern Queensland (probably), and Gulf of Carpentaria. Minor hybrid zones such as occur in this species are also to be seen in a few others, e.g. *Zosterops lateralis.*

Hybridization in Australia would appear to result from two main situations: (a) range extensions across or around arid barriers (inferring a minor improvement in the continental climate and probably some secondary adaptation to dry conditions) and, (b) outward movements made possible because of man-made alterations to the vegetation. The majority of cases are attributable to the former but the hybridization between *Gymnorhina tibicen-hypoleuca* in the Murray Valley area has undoubtedly been accelerated, if not caused, by the wholesale clearing of the land and creation of great areas of the "open field" type habitat of this species. Hybridization between *Platycercus eximius* and *P. adscitus* in the Darling Downs and northeastern section of New South Wales is presumably also partly due to these causes.

(2) Stepped Clines and Lesser Zones of Intergradation

The frequency of occurrence of stepped clines in Australia cannot, at the present state of knowledge, be judged. They too are probably not common, however.

Good examples of stepped clines are provided by the eastern and western forms of the bower-bird *Chlamydera nuchalis* in the region of the Gulf of Carpentaria, and by northern and southern forms of the goshawk *Astur fasciatus.* There is another in *Estrilda temporalis* in the Cairns-Mackay region. Certain of the minor zones of contact, e.g. in *Pachycephala pectoralis*, are possibly more correctly described as stepped clines than hybrid zones.

Various lesser races of birds intergrade in different parts of the continent but the circumstances are too little known to warrant discussion, e.g. in *Cracticus nigrogularis* in the Northern Territory and *Gymnorhina tibicen* along the Queensland-New South Wales border. In the genus *Calamanthus,* however, the intergradation of the forms *campestris* and *fuliginosus* in the Eyre Peninsula and Coorong areas of South Australia is almost certainly secondary.

Not to be confused with the above are instances of colour change along a zone of steep climatic gradient, e.g. in *Smicrornis brevirostris* and *Dacelo leachii.* No isolation has been involved here (Keast, 1957d; 1958h).

XI. THE AUSTRALIAN ENVIRONMENT OF THE PAST AND FORMER SPECIATION. ZOOGEOGRAPHIC SUBREGIONS, THE REFUGE CONCEPT, AND ORNITHOLOGICAL EVIDENCE OF PAST CLIMATIC CHANGES.

Past climatic and physiographic changes on the Australian continent must briefly be reviewed with the objective of determining if: (a) substantially different moulding forces operated during the development and radiation of the major bird groups; (b) the circumstances of origin of specialized avifaunas can be determined; and (c) factors influencing speciation in the past have been substantially different from those operating today.

Characteristics of the Tertiary, Pleistocene, and early Recent in Australia

Tertiary: The restricted information available indicates the following: (i) The continent was flat throughout and there were protracted periods of still-stand. (ii) New Guinea and Tasmania were in continuity with the mainland for part of the time. (iii) Extensive freshwater lakes occurred in the interior. (iv) Vertical earth movements initiated some of the major physiographic features of today: the Eastern Highlands or Great Divide, the Mount Lofty and Flinders ranges in South Australia, and the Spencer and St. Vincent gulfs, the latter deep coastal indentations that were to act as further barriers to west-east distribution. The Olary Ridge arose astride the southward drainage of Lake Eyre into the sea. (v) The climate was humid and warm. (vi) There was a pan-Australian, broad-leafed, mesophytic flora, for much of the period with trees such as *Cinnamomum* and *Nothofagus* prominent. In the late Tertiary, however, xeric elements like *Eucalyptus* and *Acacia* became ascendent.

Pleistocene:

(i) The continent continued to be flat. (ii) The Great Divide was further elevated in early Pleistocene (or late Pliocene), so that new erosive cycles were initiated. The Great Australian Bight was formed by down-faulting. (iii) Sea-level changes occurred in association with the glacial periods in the Northern Hemisphere, major falls of 250-300 feet twice bringing New Guinea and Tasmania into broad contact with the continent. (iv) Glaciation was negligible in continental Australia, never more than a few hundred square miles being affected. (v) Over large areas of the continent, and for a good portion of the Period, the rainfall was reasonably high. Deep alluvial deposits of Pleistocene age are known from many parts of the continent. The central lakes continued to hold water. (vi) Fossil remains show that giant herbivorous marsupials continued to range widely over the continent. Crocodile fossils are known from South Australia, and elsewhere in the south, hundreds of miles beyond their present distribution. One of the southern lungfish fossils is apparently also Pleistocene. (The Pleistocene flora, unfortunately, is virtually unknown.) (vii) The continent was subject to climatic oscillations, although the extent and number of these is not known. Various geologists, and the climatologist Gentilli (1949) have taken the view that the whole continent passed through periods of generalized wetness and dryness at these times. Possibly more generally acceptable, however, in that it accords with the theory of shifting wind belts, is that the arid belt oscillated between south and north (Keble, 1947). That is to say, whilst the south was "wet" the north may have been "dry," and vice versa.

Three to four climatic oscillations, to accord with the number of glacial periods in the Northern Hemisphere, apparently occurred. The geologist Fairbridge (1953) has suggested, however, that the rainfall would have been increased at the height of each Northern Hemisphere interglacial as well as glacial period, with each change being marked by a somewhat dry period. This would mean that the south of the continent may have had as many as eight ''pluvial periods'' of varying intensity during the Pleistocene. Apart from these considerations, however, an increase in the continental area in the north, the result of a fall in sea level, might well have had the direct effect of causing aridity over this section (C. F. Brooks, in Mayr, 1944b).

Soil evidence, believed to support the series of climatic oscillations in the Pleistocene (Butler, 1956) is now believed to refer, in the main, to later climatic fluctuations (Butler, personal comm.).

Early Recent: Widespread aridity followed the end of the Pleistocene. In northern South Australia, central Australia, and parts of Western Australia, the Northern Territory, and Queensland, there was a wholesale drying up of rivers and lakes, by now deeply silted. That the onset of the great aridity, as it has come to be called, was sudden and drastic is shown by the soils becoming freely exposed to wind erosion over a wide area (due to the inability of the plant cover to adapt quickly), and dune systems being built up (Crocker and Wood, 1947). Thus, with the advent of the Recent period the continent came to assume its present form of an arid land mass surrounded by peripheral strips and pockets of fertile country. There is uncertainty as to when the ''maximum aridity'' occurred. Provisional radiocarbon dates, however, indicate that the last of the giant herbivorous marsupials may have died out as recently as 13,000 years ago (Gill, 1955), or even 7,000 years ago (R. Tedford, personal communication).

The evidence today is of some minor climatic improvement. Dune systems are vegetated in places and there has been secondary range spread of various plant and animal species.

Former Radiation and Speciation in Australia

It is obvious that the changes in the Australian continent since the beginning of the Tertiary have been of the most profound kind. From a well-watered, well-vegetated land mass supporting a mesophytic flora, it has changed, through a series of climatic oscillations, to an arid continent on which this flora is confined to a few peripheral sections and pockets.

The original development and radiation of the Australian fauna took place under climatic conditions vastly different from those today. The nature of these earlier isolating barriers are difficult to assess.

The "great aridity" of the early Recent obviously had the most profound implications. Prominent elements like the giant herbivorous marsupials were exterminated. The then-existing flora and much of the fauna of the interior must have been eliminated or else compressed into pockets where conditions were less severe. The relict distribution patterns of animals like *Sarcophilus* (Tasmanian Devil) and *Thylacinus* (Tasmanian Wolf), whose fossils are known from western New South Wales and Western Australia, stem from this period. The lungfish *Neoceratodus* is now confined to the Burnett River, Queensland, and crocodiles to the northern coastal regions of the continent. The dryness of the Australian continent today (one-third arid, one-third semi-arid), the dominance of the dry-adapted animals and plants over the greater part, and the present-day distribution of the various vegetation formations are thus, in effect, relatively recent.

In contrast with its climate, the Australian continent has not altered physiographically to any great extent. Nevertheless, the elevation of the Great Divide in eastern Australia in the late Miocene, and its further development in the early Pleistocene has been of great significance. The Great Divide influences precipitation over a large section of the east (giving it a uniform rainfall instead of one largely confined to the winter or summer). Its presence ensures a considerable habitat diversity in the continent. All the rain forests, and most of the sclerophyll forests, are confined to it. The Great Divide is the major "refuge area" in which "fertile-country" animal species (and a good proportion of the unique endemics come in here) are able to persist. Again, many of the tropical New Guinea elements that have colonized the northeast have been able to do so because of the conditions created by the northern end of the range. The abrupt changes in climate and vegetation along the top and western slopes of the Great Divide are the limiting barrier to many species.

A second physiographic development consists of the mid- and late-Tertiary changes in South Australia: (i) the formation of the St. Vincents and Spencers Gulfs, and the Great Australian Bight, by down-faulting and, (ii) the elevation of the Mount Lofty and Flinders Ranges and of the Olary Ridge. The Bight along with climatic and edaphic factors, was to take over from the intrusive Cretaceous sea the maintenance of major floristic differences between east and west. The Mount Lofty Ranges today support a pocket of sclerophyll forest in what would otherwise be dry country. The elevation of the Olary Ridge, across the drainage of Lake Eyre into the sea, and the damming back of the steadily silting lake, must have had a local influence on animal distribution subsequently.

Little can be said of the circumstances of origin of the "specialized avifaunas" of today except that it is doubtful if any are particularly recent. It has been suggested by the writer, in contrast to the views of certain geologists who have postulated periods of fairly uniform fertility during the Pleistocene, that some desert must have been present on the continent throughout. This is because Australia has a number of unique and highly specialized desert elements, e.g. the marsupial mole (*Notoryctes*), the devil lizard (*Moloch*), and the tree *Casuarina decaisneana*. These have obviously had a long history (Keast, 1959a). The genus *Amytornis* is the nearest approach to a true desert genus amongst the birds, though there are quite a number of desert species within genera.

Much of the sclerophyll avifauna is obviously old, as are many of the savannah woodland elements. On the other hand, mangrove species and, with one or two exceptions, rain forest species, are fairly recent immigrants from the tropics.

Wood (1959) has stressed that the major Australian plant communities, though stable, are relatively young. There has undoubtedly been a long standing tendency, however, for rainfall and vegetation formations to have a zonal distribution, and for the components to bear a relative relationship to each other.

It is obvious that speciation patterns prior to the onset of aridity would not have been the same as those operative today. Nevertheless, the fact that "refuge areas" are centred on hilly or mountainous segments that have been relatively constant in position since the Tertiary (though not elevated nor eroded to the same extent) suggests that they may have, over a period, been centres of origin of new forms. As noted, the differentiation of New Guinea immigrants in Australia has been occurring continuously.

The key to much of the Pleistocene and Recent speciation undoubtedly lies in the climatic oscillations to which the continent has been subject. A much better understanding of these is needed. This particularly applies to the history of the Nullarbor arid barrier, isolating the very interesting faunas of southeastern and southwestern Australia. In this regard it has been reasoned that every south-north shift in the continent's centre of aridity would lead to a tongue of better watered and better vegetated country extending across the head of the Great Australian Bight. Speciation in some birds (*Psophodes, Eopsaltria, Pachycephala inornata-rufogularis*), various frogs (Main, Lee and Littlejohn, 1958), and tabanid flies (Dr. I. Mackerras, personal communication) would appear to be explicable only in this way — waves of east-west colonization by animal species, occurring with each improvement.

Several of the major distributional barriers of today would have been eliminated or made less effective, not only by changes in rainfall, but by changes in sea level. A relatively small fall in sea level would have rendered the Gulf of Carpentaria dry land and permitted a much greater flow of forms between the northwest and northeast. The reduction or elimination of Bass and Torres Straits must also have led to a greatly accelerated interchange of forms with Tasmania and New Guinea.

Each climatic shift in Australia has undoubtedly modified and altered the vegetation pattern. With each major change some bird species must have prospered and expanded their distribution, others become more restricted, and others undergone new adaptations. New forms and species that had developed at some isolated "point source" could have undergone marked increase in range at these times. Those that had reached species status could have come, or been forced, to occupy new habitats adjacent to those of their parents. In other cases, hybrid belts would have been formed. Lastly, amongst the various adaptations would be some with indirect evolutionary consequences, e.g. from a sedentary to a nomadic way of life, and vice versa.

The Zoogeographic Subregion Concept in Australia

The concept as it applies in Australia has recently been discussed by the writer (Keast, 1959c), and the various subdivisions as advanced by workers in the different zoological groups have been reviewed. The conclusion was reached that, so far as the concept has a place in Australian zoology, the scheme of Baldwin Spencer (1898), with its three simple subdivisions (see later), is the most natural arrangement. The Spencer scheme has recently been modified and adopted for birds by Serventy and Whittell (1951). In contrast with the Spencer scheme, the multiplicity of subdivisions advanced by some invertebrate workers were found, for the most part, to correspond to refuge areas, and areas of minor isolation, in the higher vertebrates.

The scheme of Spencer, derived originally from a study of mammals, frogs,[1] etc., is as follows:

Bassian Subregion: Forested coastal regions of New South Wales and southeastern Australia, including Tasmania. The isolated southwest corner is also rich in Bassian elements. The Bassian region corresponds closely to the limits of the sclerophyll forests in Australia.

Torresian Subregion: Forested coastal regions of the north and northeast of the continent. This element is mostly of New Guinea origin. The zone corresponds approximately to the limits of tropical rain forest and tropical savannah woodland, though elements penetrate south for varying distances down the east and west coasts.

Eyrean Subregion: Dryer interior of the continent, and extending to the coast in the south and west, especially where the arid country extends to the sea.

To what extent these divisions can justifiably be regarded as "areas of origin," as distinct from "faunistic blocks" linked by common needs in the way of climate and vegetation and adaptations to environment, it is difficult to say. The Bassian zone, as noted, is a refuge area where various old "wet country" species and forms have been able to persist. The Torresian sector retains its distinctness to a degree because it is the sector of the continent in which new arrivals from the north establish themselves. In places, the division between the regions is fairly sharp, so far as birds are concerned. This applies as between the Bassian and Eyrean species in inland New South Wales. On the other hand, the postulated line separating Bassian and Torresian elements in the coastal sector has little foundation. Individual Bassian, Eyrean, and Torresian species more often than not do not extend to the limits of their individual region but occupy only part of it. Again, and as would

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[1] In a recent comprehensive study of the Australian amphibian fauna, Dr. J. R. Moore (personal communication) has concluded that frog distribution patterns do not justify the recognition of zoogeographical subregions in Australia.

be expected, there is a varying degree of penetration by individual species from one region to another. This factor has caused Serventy and Whittell (1951) to reiterate that the zoogeographic subregion concept is only valid if used in the "fluid," rather than the static, concept.

It is doubtful if anything is to be gained, from the speciation viewpoint, in trying to analyse the Australian avifauna from the zoogeographic subregion, rather than from the vegetation formation, viewpoint. The vegetation formation is a much more real factor in bird distribution. Each of the basic vegetation formations has a series of bird species, and sometimes even groups, confined to them. These, along with an associated quota of plant and other animal species, live under common biotic and physical conditions and can readily be referred to by the terms "sclerophyll forest fauna," "savannah woodland fauna," and so on.

The Refuge Concept in Australia

Bird workers who have discussed aspects of the refuge concept in Australia include Gentilli (1949), Mayr (1950b), Serventy (1951), Condon (1954), Cain (1955), and Keast (1957e). As yet, however, no attempt has been made at a comprehensive survey or study of the major refuge areas on the continent and their characteristics. It is basic that, if the refuge theory has a real application in birds, there must be a large measure of consistency, from group to group, in the areas that have acted as "refuges."

"Relict type" distributions have long been recognised by Australian biologists: see the botanists Crocker and Wood (1947) and the entomolgist Tindale (1949) with respect to the plants and butterflies, respectively, of South Australia. It must, however, be recognised that birds, with their moderate capacity for dispersal yet reluctance to cross hostile areas, and moderate to large body size (requiring a reasonably large area to survive), are more likely to reveal what are the basic refuge areas in Australia than plants or invertebrates with little capacity for dispersal.

Figure 27 shows the major refuge areas in Australian birds as indicated by the present survey. The black arrows, and letters, indicate the barriers that isolate them.

These refuge areas have the following characteristics:

(a) Each is an area of hilly or mountainous terrain (see Fig.

3), has a higher rainfall than the surrounding country, and hence provides a measure of protection from seasonal and long-term shifts in climate. It has a distinctly richer and more diverse vegetation than its environs.

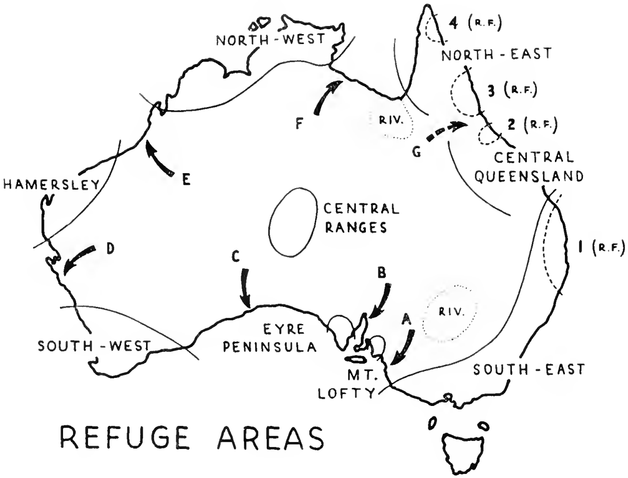

Fig. 27. Refuge areas (which are also major centres of isolation) on the Australian continent. These are typically mountainous or hilly sections, as follows: southeastern section of Great Divide, Mount Lofty Ranges, Eyre Peninsula, southwest corner, Hamersley section, northwestern section, northeast (Cape York), central Queensland, and central ranges. These are of the greatest significance in sclerophyll forest and savannah woodland species. Mangrove species are, however, isolated in the Hamersley, northwestern and northeastern segments, and a few rain forest — monsoon forest species as between the northeast and northwest.

The numbers (1-4) indicate the major rain forest refuges.

In the case of a few bird species (especially parrots) river systems have acted as refuges. The Murray-Darling basin has been of importance in a few species and the rivers entering the Gulf of Carpentaria in one.

The black arrows and capital letters indicate the major isolation barriers (see text).

In the case of a few of the parrots and one or two other bird species, river systems act as refuge areas. Riverine refuges have been earlier recognised for certain plants by the botanists Crocker and Wood (1947).

(b) Most contain more than one basic vegetation formation.

(c) Each supports several and sometimes a great number of isolated bird populations, forms, or species which in turn belong to a variety of different groups. The most distinctive forms occur between the northeast and northwest, and southwest, of the continent, respectively.

These major refuge areas, summarized in Figure 27, are as follows:

(a) *Northwest corner (especially Arnhem Land):* Many savannah woodland, monsoon forest and, to a lesser degree, savannah grassland and mangrove forms are isolated here. A number of them have reached a significant degree of differentiation. For examples see Figures 12, 21, 22 (savannah species), and 8 (mangrove species). This is also a somewhat important area in the case of plants and various other animal groups.

(b) *Northeast corner (especially Cape York):* Savannah woodland, rain forest, and a few mangrove species have isolates here. Since, however, most rain forest and mangrove forms have secondarily been derived from New Guinea, the hilly sections of Cape York have only really functioned as a refuge in the case of some savannah species. Many of the latter are counterparts of those in the northwest. For examples see Figures 12, 21, 22.

(c) *Central Queensland:* Unlike the others this is not a compact area but is somewhat vague and ill defined. That it is really a series of minor refuge areas is indicated by the multiple geographic forms in *Platycercus adscitus* and *Neositta* (Figs. 12 and 21). Again, several restricted areas of higher elevation rise above the Great Divide which is rather low here, giving rise to rain forest pockets. These areas are Atherton, the Clarke Range (adjacent to Bowen and Mackay), and Bunya Mountains.

In addition to the above, there is a degree of isolation and differentiation between various savannah woodland inhabitants of central Queensland and those of Cape York, e.g. *Seisura inquieta* (Fig. 15), *Climacteris picumnus* (Fig. 22), and *Poephila cincta*.

Central and southcentral Queensland are populated by a series of distinctive elements in the case of land snails (McMichael and Iredale, 1959), whilst several distinct species of reptiles are confined to this sector (Keast, 1959c).

(d) *Southeast of continent:* This extensive mountainous strip extends from the Bunya Mountains in southern Queensland to central-western Victoria. It is rich in endemic genera and species in all animal groups and is by far the most important of the refuge areas. Sclerophyll (mostly), rain forest, and savannah woodland elements are contained within it. At the same time, some subsections within it are of importance on their own, e.g. Macpherson-Dorrigo rain forests, Koskiusko Plateau (in invertebrates). Insular Tasmania, with its many indigenous species and races is an isolated segment. Examples include those shown in Figure 12, 21, 22.

(e) *Mount Lofty Ranges and Kangaroo Island:* These sclerophyll sections are minor refuges, and various populations isolated there have reached a minor degree of differentiation. One such is indicated in Figure 19.

(f) *Eyre Peninsula:* This functions as a minor refuge area for a couple of savannah species of southwestern origin (e.g. *Climacteris rufa occidentalis*, Fig. 22).

It fulfills a similar role in the case of various plants (Wood, 1959) and some invertebrates.

(g) *Southwestern corner:* This is an important refuge area. It contains one monotypic bird genus and a couple of dozen forms that have differentiated to varying degrees from their counterparts in the sclerophyll forests of southeastern Australia. Many others are isolated but undifferentiated. Nevertheless, its importance in birds compares in no way with that in plants, 75 per cent of the species of which are endemic to the region. About 8 monotypic reptile and 3 monotypic marsupial genera are restricted to southwestern Australia. For examples see Figures 12, 22, and 23.

(h) *Hamersley area:* Several savannah woodland and grassland bird species have morphologically differentiated isolates here, e.g. *Climacteris melanura* (Fig. 22). The mangrove forests of this section also support various morphologically differentiated isolates (see Fig. 8).

The biological significance of this area is that it contains a somewhat impoverished outlyer of the Kimberley flora and fauna, largely isolated today, mixed with a range of intruding desert elements.

(i) *Macdonnell ranges and other mountain ranges of Central Australia:* A number of savannah species have populations here that are isolated to a varying extent. Only in a couple of cases, however, has differentiation occurred and in each case it is relatively minor; example, *Rhipidura fuliginosa albicauda,* Figure 14. A number of plant species have outlyers here isolated by hundreds of miles from their counterparts in the southeast (see Keast, 1959d).

(j) *The Rain Forest refuges:* These are numbered "1-4" in Figure 27. The Cairns-Atherton tract is by far the most important and it has a large and diverse avifauna. On the other hand, the Clarke Range is apparently only of limited importance. As noted earlier, isolation and differentiation in rain forest species are mostly taking place between the Cape York, Cairns-Atherton, and Bunya Mountains-Dorrigo tracts. The isolating barriers are areas of dry open savannah.

(k) *Riverine refuges:* Where tracts of forest are developed along river systems there is a marked tendency for a richer avifauna than in the dryer surrounding country. Several of the river systems have well differentiated isolates, especially in parrots. These include those draining the Hamersley plateau, the northwest and southwest of the continent and the central ranges. In addition, the Murray-Darling system (see map) has several distinct bird forms including the parrots *Polytelis swainsoni* and *Platycercus flaveolus,* and the rivers draining the Gulf of Carpentaria have one distinct form, the parrot *Barnardius barnardi macgillivrayi.*

Barriers between Refuge Areas

The barriers isolating the refuge areas are, typically, sections or tongues of dry or arid country, as will be seen from the rainfall, climatic and vegetation maps. They are marked "A" to "G" in Figure 27. These have already been discussed in Section IX with respect to breaking up the basic vegetation formations. They may be briefly listed as follows:

(A) Coorong arid section (90 Mile Desert), a tongue of arid country extending south from the interior.

(B) Spencer Gulf, a deep coastal indentation with arid country about its head.

(C) Nullarbor Plain (arid) and Great Australian Bight.

(D) Tongue of arid country extending from the interior to the coast in the region of Shark Bay.

(E) Eighty Mile Beach arid section, a tongue of the Great Sandy Desert extending through to the sea.

(F) Tongue of dry country extending from inland to the head of the Gulf of Carpentaria.

(G) Tongue of somewhat dry savannah country extending to the sea in the vicinity of Townsville. It is easy to see how this belt, perhaps 100 miles wide, should break up the distribution of rain forest species. The fact that a few savannah woodland bird species have differentiated populations to the north and south of it suggests that it may formerly have been more severe.

The Macdonnells and other ranges in central Australia are surrounded by a series of arid tracts, the Arunta Desert to the east, Great Sandy Desert to the west, extensive gibber plains to the south, and stunted desert scrub to the north. These serve today to isolate the animal inhabitants of the central ranges from their counterparts elsewhere in the continent.

As has previously been noted, the rain forest tracts ("1" to "4" in Fig. 27) are isolated from each other by tracts of dry savannah woodland, whilst the riverine refuges are surrounded by flat, more open country.

Some Fragmental Avian Evidence supporting the Postulated Quartenary Climatic Successions

During the present survey, and elsewhere, a limited amount of avian and other evidence that appears to support the postulated south-north movements of the climatic belts has been noted. It is as follows:

Evidence that the north of the continent has been wetter than at present: (a) The distribution of the chat, *Epthianura crocea,* a species requiring somewhat damp river valleys, is now broken up into four populations, respectively 800-900 miles apart (Fig. 16). In former times this type habitat must have been much more common across the north of the continent.

(b) Many of the endemic savannah species in the north have isolated counterparts in the northwest and northeast corners of the continent, respectively (see earlier).

Evidence that the north of the continent has been dryer than at present: The isolated "species" of *Amytornis* along the northern seaboard are examples (Fig. 18a). They are derivatives of the desert spinifex species *A. striatus* and their requirements in the way of cover are such that they could only have reached their present position by a continuous tract of spinifex formerly extending through to the sea in this section.

Evidence that the south of the continent has formerly been more fertile: (a) There are a great many sclerophyll bird species with isolated counterparts in the southeast and southwest of the continent, respectively.

(b) Certain relict bird populations in the mountains of central Australia, i.e. *Rhipidura fuliginosa albicauda, Strepera versicolor centralia.*

(c) Certain "relict-type" distributions in southwestern Australia, e.g. *Atrichornis clamosus, Dasyornis broadbenti;* also the persistence of *Phaps elegans* and other species on the Abrolhos Islands, despite their occurring on the mainland only a considerable distance to the south. (Serventy and Whittell, 1951).

Evidence that the south has been dryer: Biological evidence for this is, of course, difficult to find as far as present-day distributions are concerned, for it is scarcely possible for "outlyers" of formerly widespread arid country species to survive in what are now humid zones. A possible example may, however, be the occurrence of a breeding population of the dry country robin, *Petroica goodenovii,* on Rottnest Island, the neighbouring mainland being occupied by *P. multicolor* (D. L. Serventy, personal communication). Again, the secondary range extension outwards from the southwest corner of species like *Neositta (chrysoptera) pileata* and *Acanthiza pusilla albiventris* must infer a slightly improved climate.

Certain mammalian fossil occurrences are significant. L. Glauert (personal communication) has recorded remains of the dry country bandicoot, *Macrotis lagotis,* in post-Pleistocene cave deposits at the Mammoth Cave, southwestern Australia, where the animal no longer occurs. Similarly, Lundelius (1957) found fossil *Dasycercus,* an arid country dasyurid, as well as *Sminthopsis hirtipes,* in caves north of Perth, many hundreds of miles south of their present desert habitat.

In contrast with the above, Tindale (1949) and Condon (1954) take the view that the persistence of a few relict bird and butterfly populations in South Australia indicate that the climate in this section could not have been materially dryer in the recent past.

Evidence that the south of the continent has been subject to more than one "climatic swing." Evidence for this comes from frogs (Main, Lee and Littlejohn, 1958), tabanid flies (Dr. I. Mackerras, personal communication), birds like *Psophodes olivaceus-nigrogularis* (map in Keast, 1958g) and *Pachycephala rufogularis-inornata* (see Fig. 13), and *Eopsaltria georgiana-australis*.

More examples of double invasion of the southwest by sclerophyll forest bird species might be expected than actually occur. *Eopsaltria georgiana* and *E. australis griseogularis* is, however, a good case of this. The red-backed wrens of the *Malurus lamberti* complex (*M. elegans* and *M. pulcherrimus*) might well be a second, and the zonal races of the thornbill *Acanthiza pusilla* in the southwest, a third.

The way in which various bird genera are represented by distinct species in adjacent and "parallel" vegetation zones could, in point of fact, be evidence of climatic "swings." These species could only have arisen in isolation (possibly during arid phases) and presumably become preadapted to the second habitat prior to the changing climate permitting them to spread out through it as it expanded. It will be noted that Paramanov (1959) has postulated shifts in the temperature zones in association with glaciation to account for the altitudinal zonation of certain fly species in the Australian Alps.

Soil-Vegetation Relationships and the Climatic Past

Soil, next to climate (present and past) and topography, is the chief factor governing the distribution of vegetation. Accordingly, it can be said that the edaphic history of an area and the distribution of the major soil areas today have a basic influence on present day animal distribution. Alternatively, the major soil changes during the Tertiary and Quaternary must have also had a direct bearing on past animal distribution.

As has been noted, the zonal soil groups in Australia follow a similar pattern to rainfall, as will be seen from a comparison of Figures 5 and 6. That they follow a broad but not absolute correlation with much of the zonal vegetation sequence has been stressed by Wood (1959) and others. The maps indicate that this correlation is best between sclerophyll forest and the podsols, mallee and the mallee soils, desert loams and mulga, and desert sandhills and desert grassland.

Soils are highly complex and variable substances and their development and evolution are conditioned by many factors, including parent material, age of land surface, relief, climate (rainfall and temperature), vegetation, and even the fauna.

Again, most soils are polygenetic, the result of more than one combination of soil-forming factors (Crocker, 1959b). The physiographic and climatic changes outlined for Australia have thus, obviously, had a direct influence on soils: mountain building, sedimentation, erosion, wind, vulcanism, fluviatile and arid periods, climatic and rainfall shifts, and plant growth itself. Hence, it must be stressed that a simple rainfall change does not permit the biologist to assume that this would automatically lead to the development, over that section of the continent, of the vegetation association that exists in the equivalent rainfall zone today. The influence of the change may, in point of fact, be direct, or it may be indirect and dependent upon a vegetation or microbiotic succession first creating the necessary soil nutrients.

Unfortunately, little more has as yet been learnt of past soil changes in Australia than of past vegetation changes. Edaphic factors serve to explain the most puzzling, and certainly the most important barrier to plant and animal distribution in Australia today, that serving to isolate the forests of southwestern Australia from those of South Australia and the east. This isolation, originally associated with the Cretaceous and, to a degree, Tertiary seas, has been shown by Crocker and Wood (1947) to have been successfully retained long after the disappearance of the physical barrier by (a) the southwestern forests being specialized for life on lateritic soil, (b) the accession of calcareous loess during the late Pleistocene, resulting in a large area of pedocalcyc soils lying right across their potential routes of colonization to the east plus, of course, the climatic factors already discussed.

XII. "ECOLOGICAL" SPECIATION. THE DEVELOPMENT OF HABITAT DIFFERENCES BETWEEN SPECIES

It has been stressed that the habitat occupied is a "species character" in the case of most Australian birds. Hence, it is important to endeavour to explain the origin and development of these ecological differences.

Two approaches could give this basic information: (1) A survey of the species to show if any vary geographically in habitat occupied (in the way that they vary geographically in morphological characters) and, (2) A study of the ecology of related species occupying adjacent habitats. This should reveal just how great the differences between them actually are and how they might have arisen.

The latter approach obviously requires detailed field studies and hence can only be lightly discussed here. It is, however, a profitable field for future investigation.

Geographic Variation in the Habitat occupied by Species

(a) Habitat Versatility in Species with Broad or Generalised Ranges

Whilst some species are restricted to one vegetation formation, others extend through many, sometimes ranging widely over the continental land mass. In these cases it is to be expected, since the physical and biotic conditions will vary, that extreme populations will differ in their adaptations. Isolation is lacking in species with wide and extensive "interior type" distribution patterns and is unlikely to arise.

However, as suggested by various authors, the severance of any continuously ranging species into two parts would consolidate and increase the ecological differences between the extremes.

(b) Habitat Variation in Species with Peripheral or Specialized Ranges

As noted, it is in these species that the majority of morphologically differentiated isolates occur. Here too many significant cases of geographic variation in habitat accompanying speciation are to be found. A selection of these is as follows:

(i) Within Species

Rhipidura fuliginosa and *Pachycephala pectoralis:* These two species extend, with various isolates, almost completely around the periphery of the Australian continent. Sclerophyll forest is occupied in eastern and southwestern Australia, rain forest in the northeast, monsoon forest in the northwest, and mangroves in the west. *Pachycephala* also occurs, in places, in mallee and *Rhipidura* has an isolated outlyer in the Macdonnell ranges. This habitat variation in *Rhipidura fuliginosa* will be seen in Figure 14.

The common denominator of these habitats is dense cover. Otherwise they have relatively little in common.

Eopsaltria australis and *Climacteris rufa:* Both of these species have a fairly wide habitat tolerance in southwestern Australia, though their headquarters are the sclerophyll forests.

Each has an isolated outlyer in the savannah woodland on Eyre Peninsula to the east of the Nullarbor Plain.

Climacteris leucophaea. This species occupies sclerophyll forest in eastern and southeastern Australia, rain forest in the Cairns-Atherton sector, and mountain forest in New Guinea (see map in Keast, 1957e). The north Queensland and New Guinea races are isolated. The rain forest form (*minor*) is approaching that stage of differentiation typical of a full species.

Strepera versicolor. This is a mountain species in the south east, but it has a derivative in the dry mallee of western Victoria.

Stipiturus malachurus. This species, basically an inhabitant of submarshy heathlands along the coastal fringe, provides an interesting demonstration, in the western part of its range (Fig. 19), of the adaptational pathway to life in the semi-arid mallee and arid spinifex desert.

A derivative, *S. ruficeps*, is isolated in the spinifex desert of the centre of the continent.

(ii) Within Superspecies

Sericornis frontalis — S. humilis — S. maculatus: The habitat in this group extends from rain forest and sclerophyll forest in eastern Australia to dry sclerophyll, savannah woodland, and coastal thickets in the south and southwest of the continent.

Calamanthus fuliginosus — C. campestris: The former inhabits the damp peripheral coastal section, the latter the semi-arid and arid inland. There is a morphological and habitat transition zone in South Australia.

Psophodes olivaceus — P. nigrogularis: The former occupies the wet rain and coastal sclerophyll forests in the east. The latter occupies the coastal thickets and adjacent sclerophyll in the southwest, and the semi-arid mallee of that section and of inland Victoria. That is to say it demonstrates the transition from life in wet to life in dry country (Keast, 1958g).

Amytornis striatus: Here the parental form has an extensive range through the spinifex sandplains of the interior. From it isolated species that live in rock river gorges have been "budded off" around the periphery of the range (Fig. 18a).

Malurus cyaneus — M. melanotus — M. splendens group: In this case a chain of 4 distinctive forms (3 of which are certainly so distinctive that they must be regarded as species) are *isolated* in a series of climatically quite dissimilar habitats from east to west across the continent (Fig. 8). These are: *M. cyaneus* (eastern sclerophyll forests); *M. melanotus* (inland mallee and mulga), *M. callainus* (central spinifex desert), and *M. splendens* (western sclerophyll forest and dry scrub).

Climacteris erythrops — C. affinis: These species are isolated in mountain sclerophyll in the east and arid mulga in the interior, respectively.

Drymodes brunneopygia — D. superciliosus: The former is isolated in the dry mallee association of the interior of southern Australia, the latter in the rain forests of Cape York and New Guinea.

The above instances show not only that the different races of a species (isolated or otherwise) may occupy distinct vegetation formations in different parts of the range but how these habitat differences may develop. Geographically representative species within superspecies sometimes occupy vegetation formations that are almost the opposite extremes of each other.

These cases indicate the probable mechanism whereby adjacent vegetation formations or zones come to be occupied by different members of a genus. It is characteristic of most species to extend outwards to the limits of the occupiable habitat. Where there is geographic variation in habitat the process is, in Australia, not one of the species varying its "preference" from one part of the range to another but of occupying the only vegetation formation available. As with purely morphological characters, isolation tends to consolidate and increase the differences. Thus, for example, amongst sclerophyll forest species *Climacteris rufa* has an isolate in savannah woodland whilst *C. leucophaea* has one in rain forest.

Once an isolate develops habitat differences from its parent, further changes can, presumably, take place in two ways. The habitat to which it is confined could undergo further change or modification, necessitating further adaptive changes on the part of the bird, if it is to survive. Eventually a situation could develop, as in the *Malurus cyaneus* superspecies or *Climacteris erythrops*, in which the different species, isolated from each other, occupy very different habitats. Alternatively, climatic changes could secondarily bring the vegetation formations into a closer position relative to each other so that the forms occurring in them approach or meet along the periphery.

If reproductive isolation has been established in the meantime, one consequence could be that each would remain within, or at least have a preference for, the formation to which it had become adapted. The honeyeaters *Meliphaga melanops* and *M. cassidix* in southern Victoria apparently avoid competition by this mechanism, and it will probably prove to be equally the case with the coastal and interior races of the thornbill *Acanthiza pusilla* in New South Wales.

Competition may, in actual fact, be the final force consolidating habitat differences between related species (see next section).

It goes without saying, in all these cases, that before a species can adapt or develop into a new association that habitat must contain certain characteristics basic to that species. Thus, members of the genus *Malurus* require, at all times, thickets or undergrowth and those of *Climacteris* tree trunks on which to feed. Nevertheless, at a certain stage, feeding and other modifications may manifest themselves, e.g. members of the *Climacteris picumnus* group occupying open country obtain part of their food from the ground.

Some geographic variation in habitat and ecology is undoubtedly characteristic of all widely-ranging species. Those members of sclerophyll species living in southwestern Australia, for example, are subject to somewhat dryer conditions than their counterparts in the east. Alternatively, within any one area, the vegetation is subject to change from time to time, as part of a succession or due to a changing climate.

All in all, it can be said that there is ample indication in Australia of how isolates may diverge and "speciate" ecologically, just as they do morphologically. Some ecological differentiation probably precedes geographic isolation in most instances but there is no need for it to do so.

(c) The Occupation of Adjacent or Nearby Habitats by Different Infraspecific Forms

Instances of this are apparently not uncommon in various montane regions of the world where sharp altitudinal changes in vegetation, and the interdigitation of vegetation zones bring markedly different bird habitats into close proximity. The mountain chains of California provide one such example — see the various publications of Miller and others (e.g. Miller, 1951). These are the kinds of situations that are sometimes considered to be possible instances of sympatric speciation. Ornithologists generally, however, are adamant that sympatric speciation does not occur in birds.

Australia, with its general flatness and arrangement of vegetation formations into broad zones, provides little evidence of this type of race distribution, for barriers are generally broad, not narrow. Speciation is thus clearly seen to be geographic. The nearest approach to the other situations, however, are to be seen in the following cases:

(i) Colour races associated with steep climatic gradients (examples of Gloger's Rule). Examples: *Smicrornis brevirostris* and *Dacelo leachii.* These are purely local clinal forms, however, without a potential for developing into new species.

(ii) Zonal races, in which isolation is present. There are a couple of instances of these in New South Wales. *Acanthiza pusilla* and *Malurus lamberti* each have a coastal race (in sclerophyll) and an interior one (in savannah, etc.). Both are now isolated from their counterparts (though in *Malurus* there is a hybrid zone in northern New South Wales). The interior race of *Acanthiza pusilla* is certainly a secondary invader of eastern Australia for its affinities lie with the southwestern stocks (Mayr and Serventy, 1938).

Another such case is provided by the Samphire Thornbill (*Acanthiza iredalei*) in South Australia (Condon, 1954). Here, three races are isolated in adjacent but different habitats; i.e. it is the same kind of situation as in the species of the *Malurus cyaneus* group (Fig. 8).

Less understood than the above are the colour races (three) of *Acanthiza pusilla* in southwestern Australia (Mayr and Serventy, 1938; Serventy, 1953). As their distributions correspond to general zones of decreasing rainfall their characteristics could be attributed to the Gloger Effect were their ranges not paralleled, to a degree, by three species in the *Malurus lamberti* group of wrens. In the later publication, Serventy (1953) has suggested that the coastal race, *Acanthiza pusilla leeuwinensis,* may actually be derived from the coastal one in the east, by migration around the Bight, and that it has achieved its present resemblance to the inland one by secondary gene flow between them.

Ecological Differences between the Different Members of a Genus Inhabiting the same or Adjacent Habitats

(a) The General Problem: the Situation in "Old" and Well Consolidated Species

The Australian avifauna contains many instances of species within genera specialized for life in different vegetation formations, vide *Meliphaga, Malurus, Gerygone, Climacteris* (Figs. 7, 8).

Some of the larger genera, moreover, have more than one species within a single vegetation formation, e.g. *Meliphaga* and *Acanthiza* in the sclerophyll forests near Sydney. In such cases distinct subzones are occupied. Here, different species of *Meliphaga* inhabit, respectively, the stunted heathlands of the hilltops, areas of saplings and undergrowth, the more open sections of the forest, and pockets of rain forest. Of the five species of *Acanthiza* occurring in the area, two are ground feeders (in different classes of country). One is mainly a low bush and shrubbery feeder. The other two are foliage feeders, with a tendency for the one to inhabit mainly somewhat lush forests in hilly sections and the other dryer sections in more open country. These observations reflect findings from other parts of the world that related bird species occupy slightly different habitats or niches and that direct food competition between them is rare, e.g. Europe (Lack, 1944), East Africa (Moreau, 1948), and California (Miller, 1951). As yet no comparative work on the finer ecological attributes of related bird species has been carried out in Australia. It could be, however, in view of their generalized similarity in bill form, that in most cases no more profound food differences separate the occupants of adjacent habitats than those directly associated with the habitats themselves. Most bird species are now recognised as being somewhat opportunistic feeders (Lack, 1954; Hinde, 1959, and others). Where, however, closely related species co-exist in a single habitat they tend to be specialized for different foods (Lack, 1954).

(b) Recently evolved Species. Habitat Differences in cases of Marginal Overlap and Double Invasion

In all cases of marginal overlap of recently evolved species in Australia there is at least some tendency for different habitats to be occupied. This indicates not only that slightly different "preferences" have been built up during the isolation but emphasizes the role of competition in consolidating, if not initiating, ecological differences.

The habitat relationships in the overlap area in the cases of recently evolved species are as follows:

(i) *Amytornis textilis* and *A. modestus* (Fig. 17a) in the Macdonnell Ranges. The former lives in spinifex on the hills and the latter (which is apparently the invader) keeps to spinifex in the valleys. Elsewhere, similar or equivalent habitats are occupied.

(ii) *Philemon argenticeps* and *P. novaeguineae* (Fig. 26) in northern Australia. In this instance the former, the older resident in Australia, occupies the savannah woodland and grassland belts extending, in places, well out into the dryer forests. The later invader keeps to the peripheral mangroves and damper savannah woodlands of the coastal strip.

(iii) *Meliphaga virescens* and *M. versicolor* (Fig. 25). In this case the parental species (the former) occupies the dryer interior and its derivative (which arose in New Guinea) has re-entered Australia to occupy the mangrove habitat.

(iv) *Melithreptus lunatus* and *M. albogularis* (Fig. 23). In eastern Queensland, where these species overlap, the former (the southern species) keeps to the highlands and the latter (the invader) to the lower country.

(v) *Meliphaga lewini* and *M. notata* (Fig. 24). These two species have the same sort of relationship in the Atherton area, where they overlap. The southern *M. lewini* is only to be found in the highlands.

(vi) *Pachycephala rufogularis* and *P. inornata* (Fig. 13). The former occupies a very restricted, and presumably specialized, area in the mallee of eastern South Australia — western Victoria. The latter has a wide range and extends well beyond the limits of the mallee.

(vii) *Acanthiza ewingi* — *A. pusilla* and *Pardalotus quadragintus* — *A. punctatus*, cases of double invasion of Tasmania. In each genus the earlier invader (the first named in each case) has the more restricted habitat and range as well as being the rarer form. Thus, *Acanthiza ewingi* is chiefly an inhabitant of the "deeper forests and scrub" and *Pardalotus quadragintus* has a very "patchy" distribution (Sharland, 1945). The later arrivals have a wider, more continuous range and generalized habitat requirements.

(c) Interspecific Competition and its Influence on Habitat Plasticity

This subject is to be treated in detail elsewhere, and hence will only briefly be reviewed here.

Two situations that have now been recognised in various parts of the world have a series of Australian parallels. These are:

(i) The occupation of broader habitat zones in regions where there is no closely related competitor or, as it is sometimes expressed, greater "ecological tolerance" in such situations.

(ii) The occupation of the same or equivalent niche by distinct species in different areas.

Quite exceptional examples of these are to be found in the isolated sclerophyll forests of southwestern Australia, a section of the continent that might be described as a "forest island." It has an "unsaturated fauna" with fewer than 70 per cent of the species that occur in an equivalent section of the southeast. Presumably this is because only a proportion of species ever succeeded in reaching there, although some secondary extinction cannot be overlooked. The genus *Climacteris* (tree-creepers) is represented in eastern Australia by three species, one inhabiting mountain sclerophyll, one lowland sclerophyll, and the third savannah country. Only one species occurs in the southwestern corner (*C. rufa*) and it occupies wet and dry sclerophyll and savannah woodland, extending into the mallee association. *Gerygone* (arboreal warbler) is represented by three species in the southeast of the continent (but one of these lives in rain forest, an association absent from the southwest). The other two inhabit sclerophyll forest (*G. olivacea*) and dry savannah (*G. fusca*), respectively. In the southwest, however, where only the latter occurs, it inhabits both associations.

The Meliphagidae are represented by less than half the number of forest species found in the southeast. There are several significant cases of change of habitat to fill vacant niches. *Lichera indistincta* and *Meliornis novaehollandiae*, mainly mangrove and "stunted heathland" species, respectively, in southeastern Australia, are forest dwellers here. *Meliphaga virescens*, a strictly dry country and desert species in the east, in the absence of such related species as *Meliphaga chrysops, M. fusca,* and *M. melanops,* is the common forest honeyeater in the southwest. A specialized nectar-feeding marsupial (*Tarsipes*), with elongated snout, tubular lips, and brush-tongue has developed in southwestern Australia, the only place where such an ecological form occurs. This may well have been associated with the paucity of nectar-feeding birds there (Meliphagidae, Loriinae).[1] Lastly, an interesting case of ecological shift occurs in the thornbills, *Acanthiza,* in southwestern Australia. Here, there are only three species instead of five in any equivalent section of the east . Of the latter, two are foliage feeders (*A. lineata* and *A. nana*), two are ground feeders (*A. chrysorrhoa* and *A. reguloides*), and one (*A. pusilla*) is an intermediate feeder. The foliage feeders are, however, absent in the southwest where one of the ground feeders, *A.* (*reguloides*) *inornata,* has largely adapted to the vacant niche.

These examples of ecological replacement and displacement reflect those recorded in the Galapagos islands (Lack, 1947) and Hawaiian Islands (Amadon, 1950b, p. 246), and elswhere.

A search of the Australian avifauna reveals a variety of instances of equivalent habitats being occupied by different species in various parts of the continent. These occur in genera that have geographically representative species, e.g. in the honeyeaters (*Meliphaga*), and in finches belonging to the genus *Poephila.* More striking cases, however, are to be seen relative to some of the more specialized ecological "niches," thus:

(i) Trunks and branches of trees. Over the bulk of the continent this food niche is occupied by members of two genera, the tree-creepers (*Climacteris*) and nuthatches (*Neositta*). The bills of these birds are long and straight for the extraction of insects and spiders from the cracks and fissures, and they have strong feet and claws for supporting themselves in vertical positions. Neither group occurs in Tasmania (though there are a few sight records of individual tree creepers). Here, a large billed honeyeater (*Melithreptus* (*gularis*) *validirostris*) spends much of its time searching the bark (Sharland, 1945). Again, in the dense rain forests of Cairns-Atherton, only one species

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[1] The southwest has however, a much larger number of *species* of nectar-bearing shrubs than the southeast. These may well provide a more consistent nectar-flow from month to month and hence it may be this that has permitted the development of a specialized nectar-feeding marsupial.

of *Climacteris* occurs, *Neositta* being absent. A flycatcher, *Arses kaupi,* has here developed the habit of hunting over the trunks for insects.

(ii) Masses of eroded rock in gorges, in which fissures and caves occur. This niche might be typified by that of the cave-warbler, *Origma rubecula,* endemic to the sandstone-limestone area near Sydney, which finds its insect food about the rocks. In the Macdonnell Ranges in central Australia, however, a grass-wren, *Amytornis textilis,* has the same habits and food niche, and in northern Australia members of the *A. striatus* group behave in the same general way. In the Carnarvon Ranges of central Queensland, an area of sandstone similar to that near Sydney, the scrub-wren *Sericornis frontalis,* passingly utilizes the vacant niche.

Adaptations such as those outlined in this section stress the great versatility and adaptability of many birds with respect to habitat. They indicate how the ecological changes associated with adaptation to a new habitat coincident with speciation may be made. The competition of closely related species may, moreover, serve to consolidate habitat differences.

XIII. CONTINENTAL AND ARCHIPELAGO SPECIATION COMPARED

Quantitative Differences between Continent and Archipelago

The 425 bird species covered in the survey, only 70 of which actually range beyond the continent to any degree, have a total of 485-505 morphologically differentiated isolates in the section to the east of Wallace's Line (Timor, Palau, Samoa and New Zealand), and 211-226 isolates within Australia (Table 3). For a comparison of the "potential" of an archipelago and a continent for giving rise to new species, however, an area of the southwest Pacific of equivalent size to that of Australia, and which excludes New Guinea (that has partly a "continental-type" of speciation) must be taken. Such is shown in Figure 28. It embraces the Bismarks, the Gilberts, Solomons, Fiji, New Hebrides, and New Caledonia.

The bird species (53) occurring both in this area and in Australia, and the number of morphologically differentiated isolates in each, are set out in Table 10. The number of isolates in the island section is 201 and that on the continent 38-43; the island segment, significantly enough, has some five times as many. Several of the species, moreover, have an exceptionally large number of isolates in the archipelago region. Thus, *Accipiter novae-hollandiae* has 9; *Rallus philippensis*, 12; *Halcyon chloris*, 26, *Coracina tenuirostris*, 10; *Rhipidura rufifrons*, 18; *Petroica multicolor*, 10; and *Pachycephala pectoralis*, 34. These substantially account for the greater number of differentiated forms in the Pacific area. That the trend is, however, a general one is shown by the fact that only in three species does the number of continental isolates exceed the archipelago ones: *Butorides striatus*, *Turnix varia*, and *Rhipidura fuliginosa*. The last two of these extend for only a short distance into the archipelago area.

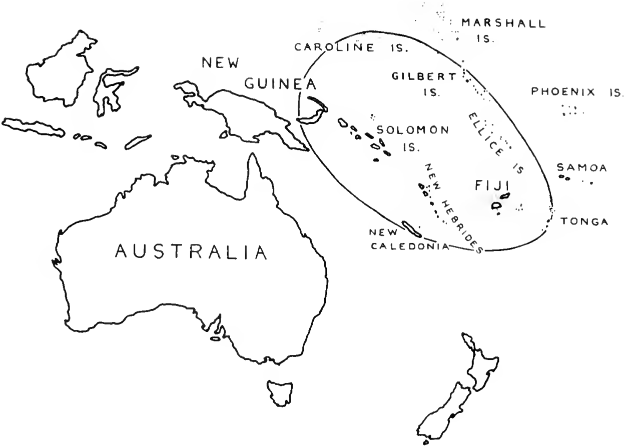

Fig. 28. Australia and an archipelago area of equivalent size in the southwest Pacific (enclosed by plain line) to compare potential for giving rise to new species.

Qualitative Differences between Continent and Archipelago

Since the days of Darwin and Wallace workers have been impressed by the striking and often bizarre appearance of insular races and species. This not only applies to the more isolated archipelagos like the Galapagos and Hawaii but is seen, to a degree, over a wide section of the southwest Pacific. The studies on *Rhipidura rufifrons* (Mayr and Moynihan, 1946), *Petroica multicolor* (Mayr, 1934), *Artamus leucorhynchus, Lichmera indistincta*, and others may be noted in this regard. It also often applies in the case of islands lying offshore from a larger land mass, as in the genus *Tanysiptera* in the New Guinea region (Mayr, 1954b). Bird species that do not vary at all on the Australian continent may have distinct populations on peripheral islands, e.g. *Dicaeum hirundinaceum, Poephila guttata*. Compared to many of these insular forms, continental variation is commonly minor and insignificant — an observation that, as noted, led Goldschmidt (1940) to believe that evolutionary processes on the two were dissimilar.

Archipelago and insular bird populations are commonly characterized by: (a) Marked shifts in colour pattern and in the distribution of body colour. (b) Shifts in the degree of sexual dimorphism within species. (c) Changes in the size and form of appendages, especially the bill and tail. (d) Changes in over-all body size.

The present survey reiterates the greater prominence and frequency of these changes under archipelago conditions. It also shows, however, that:

(a) All these different kinds of variation occur, to a degree, on the Australian continent. Marked shifts in colour pattern are typical of isolates of long-standing, e.g. as between the southeastern and southwestern populations of the finch superspecies *Zonaeginthus bellus* and the honeyeater *Acanthorhynchus tenuirostris*. Shifts in the degree of sexual dimorphism are minor and rare but occur in the whistler *Pachycephala pectoralis*, some of the wrens (*Malurus*) and as between species of the bower-bird genus *Chlamydera*. There is a marked case in the *Petroica cucullata-vittata* group but in this case Bass Strait has been the isolating barrier. Changes in bill-form in association, apparently, with a change from insect to seed-feeding, occur in *Amytornis* and *Turnix*, whilst a noticeable elongation of bill is seen in the case of certain nectar-feeding honeyeaters. For example, note the difference between the generalized bill of *Meliphaga fusca* and the elongated one of *M. macleana* (figured in Keast, 1959e). Differences in body size between closely related members of a genus are not common but do occur in *Amytornis*. Within species, continental size variation typically takes the form of a south-north cline of decreasing body size.

The trend is accentuated, with individuals from the southernmost and northernmost areas averaging a difference in size of 20 per cent or more, when the end populations are isolated from each other, e.g. in *Scisura inquieta* and *Megaloprepia magnifica*.

(b) Much of the archipelago and insular variation is also only minor. The more striking forms are, on the whole, in the minority.

Notwithstanding the above, it is a reasonable assumption that the small insular populations, morphologically distinctive though they may be, are over-specialized. They would probably have little future in the event of a marked change in their biotic environment, or were they introduced to the competitors and predators of a continent. It is with the generalized and versatile continental populations that the real future of each evolutionary line lies.

Comparison of the Continent and Archipelago as a Physical and Genetic Environment

Tropical and subtropical archipelagos differ from continents in various ways. Rainfall tends to be regular, if seasonal. Temperatures are equable. The rigorous climate that necessitates extensive latitudinal migrations or nomadic movements is lacking. There is necessarily a year-round supply of food available. The shore line sharply limits the range.

Archipelagos also differ from continents in that, resulting from the reduced opportunities for dispersal, they have only a fraction of the animal and plant species. A corollary is that potential food niches are likely to remain unoccupied on remote islands, simply because the right species are unable to reach them. This means, of course, that species are less likely to be confined, by competition, to a restricted way of life but can more easily diversify or become modified to a new niche. More strikingly, this same absence of competition has permitted and encouraged the bizarre radiation by the members of single groups that occurs on the Galapagos and Hawaiian islands.

The big problem in archipelago speciation is to explain how so many distinctive forms can develop on adjacent islands when, as environments, they are apparently similar. This was a subject that much occupied the mind of Darwin (1890, p. 355) and he sought to explain it away in terms of the biological, not the physical environment, thus: "How has it happened in the several (Galapagos) islands situated within sight of each other, having the same geological nature, the same height, climate, etc., that many of the immigrants should have been differently modified, though only a small degree. This long appeared to me a great difficulty; but it arises in chief part from the deeply-seated error of considering the physical conditions of a country as the most important for its inhabitants; where it cannot be disputed that the nature of the other inhabitants with which each has to compete is at least as important, and generally a far more important element of success.''

Mayr (1947), in quoting Darwin, stresses that individual islands in an archipelago are not as similar as they might at first appear but may differ in size and elevation, temperature and precipitation, ocean currents and, since their population by fauna and flora is fortuitous, as biotic environments.

Amadon (1950b) in a review of the remarkable modifications in the bill form of the Hawaiian honey-creepers comments on ''rapid divergent evolution'' in archipelagos and quotes Simpson's views that ''quantum evolution'' is associated with a change from one ecological niche to a radically different one. Such an explanation, however, can hardly account for the lesser changes in colour and colour pattern that characterizes so many of the insular forms in the southwest Pacific. Nor, since few of the populations are very small, is genetic drift (the fixation of hitherto neutral or unfavourable genes merely by chance) likely to play a major role.

An interesting theory has recently been advanced by Mayr (1954b) to account for the accelerated variation and differentiation in animal populations on islands adjacent to continents. This is, in effect, that insular populations, by nature of the fact that their founders could only possess a limited proportion of the gene reservoir of the species, have a different genetic ''environment'' than their parental forms. An all-important factor in the transition from one well integrated and conservative condition, through a highly unstable period, to another new period of balanced integration, lies in what genes are carried to the new areas by the founders. That the new complex will be different is assured by the following considerations: (a) As noted, the founders represent, genetically, only a segment of the parental variability; (b) alleles that had been previously of equal viability are likely to change their relative viability during the period of rapid readjustment; (3) recessives will have a much greater chance to become homozygous in the reduced population and thus become more exposed to selection.

XIV. SUMMARY

(1) The present study is a detailed investigation of species-formation in the Australian avifauna. It covers 425 (80%) of the 531 species of breeding land and freshwater birds occurring on the continent.

(2) Monotypic species (that do not vary geographically) amount to 188 (44%), whilst 99 (23%) have clinal variation only. Those with morphologically differentiated isolates on the continent total 138 (33%).

(3) The number of morphologically differentiated isolates, forms with the "potential" of developing into new species, totals 211-226, an average of 0.5 per species for the whole fauna, or 1.6 per species for the 138 that have them. Sixty (23%) of the isolates have differentiated to a marked or moderate degree.

(4) The continent is rich in demonstrations and examples of currently occurring speciation. Ten families provide examples of the full range of intermediate stages from isolated populations that have not yet differentiated to markedly different isolates and examples of range overlap, without interbreeding, of newly-evolved forms. An additional 8 families show examples of all stages but the last.

(5) Almost one-third of Australian bird species belong to superspecies. Many of these superspecies groups are entirely confined within the continent. There are about a dozen current cases of range overlap by newly evolved species, and about the same number of instances of (current) speciation by double invasion. (There are also various instances of successive invasion of an area by infraspecific forms.) Most of these invasions are from New Guinea to Australia and from the mainland to Tasmania. There is one good case of speciation by circle formation, with the end-members of a chain of forms infertile.

(6) The habitat (vegetation formation) occupied by a species, and the nature of a species' seasonal movements, individually exercise a strong influence on its potential for giving rise to isolates and hence new species. The family grouping to which it belongs, however, appears to have little influence, other than through what might be called the "ecological attributes" of that family. Of the total isolates in Australian birds, 14 per cent are to be found in species that are basically inhabitants of rain forest, 33 per cent occur amongst the sclerophyll forest dwellers, and 20 per cent belong to savannah woodland species.

much speciation occurring as between (i) the rain forest segments of Cape York, Cairns-Atherton, and south Queensland- These vegetation formations are peripheral in distribution and are broken up into isolated tracts. In contrast to this, few isolates occur in species specialized for life in the interior, continuously ranging, vegetation formations.

Nomadic bird species, amounting to some 23 per cent of the whole avifauna, have only an insignificant number of morphologically differentiated isolates. The overwhelming majority of isolates occur in the sedentary species. Virtually no isolates occur in the hawks and large water birds, which species are typically nomadic.

(7) The geographic isolating barriers leading to isolation and differentiation are discontinuities in the basic habitat (vegetation formation) of species. These are either tongues of dry or arid country that extend from the interior to the sea to break up the forested areas, or are tracts of sea. The way in which these barriers operate is discussed in detail. There is New South Wales, respectively, (ii) the sclerophyll forest tracts of southeastern Australia, Tasmania, and southwestern Australia and, (iii) the savannah woodland tracts of northwestern and eastern Australia. Differentiation is common between populations of species on either side of Torres Strait. It sometimes occurs on offshore islands. Further afield, a variety of Australian species have distinctive populations or counterparts in New Zealand, Lord Howe Island, and New Caledonia. Others have given rise to many insular forms in the archipelago areas of the southwest Pacific.

(8) The present study discloses the existence of about 33 hybrid zones, representing the premature re-uniting of differentiating forms. Most result from a minor climatic improvement that has permitted forms to spread out. The clearing of the forests has been a relevant factor in other cases. The geographical position of the various hybrid zones is discussed, it being pointed out that most occur between the main centres of isolation and differentiation (i.e., "refuge areas").

(9) The Australian climatic and physiographic environment of the Tertiary, Pleistocene, and early Recent, are reviewed. Much of the original radiation and speciation in birds took place under conditions of generalized fertility. Present-day aridity is a relatively recent development. The circumstances of Tertiary speciation cannot be seen. During the Pleistocene,

however, successive eras of range extension and isolation must have accompanied the periodic climatic shifts of the period. The "refuge area" type of isolation of today possibly occurred to a degree previously. The position of the refuges, peripheral mountainous or hilly areas, would have been the same because there has been virtually no mountain-building since the end of the Tertiary.

Since the distribution, and composition, of the basic vegetation formations (that compose the bird habitats) are dependent on the soil substratum, as well as rainfall, it is not valid to assume that any particular shift in the rainfall belts would alter the habitat distribution to the same degree. The soil itself is an evolving system. In the ultimate degree, the birds (their distributions and adaptations), the vegetation formations and their individual members, the soil, and the climate are all changing, individually and relative to each other. Nevertheless, through the habitat, rainfall and soil changes have a direct influence on bird distribution and speciation.

Colonization from, and by way of, New Guinea, and subsequent differentiation in Australia, have made a significant contribution to the building-up of the Australian avifauna, not only in recent times, but throughout geological history.

(10) "Ecological" speciation, the development of habitat differences between species, is reviewed in some detail. Cases of geographic variation in habitat occupied and habitat "differentiation," under circumstances of isolation, are discussed. It is noted that where marginal overlap and double invasion occur the two species separate out into slightly different habitats, notwithstanding that they occupy similar habitats elsewhere in the range. Likewise, species tend to occupy much broader niches where there is no competitor.

(11) Differentiation and speciation on the Australian continent is compared with that occurring in an archipelago segment in the southwest Pacific of equivalent size. It is found that there are five times as many morphologically differentiating isolates in the latter. Though much of the insular isolation is minor, studies on species like *Rhipidura rufifrons* and *Petroica multicolor* reiterate that insular populations tend to be subject to more marked shifts in colour pattern, in the degree of sexual dimorphism within species, and significant changes in size and form of appendages.

(12) To sum up, speciation is actively occurring in Australian

birds and the number of forms with the "potential" of developing into new species is large. All speciation is geographic. At the same time, the same basic factors and rules apply as in the island archipelago from which much of our basic knowledge of the speciation process has been built up.

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The present study was carried out in 1953-1955 when the writer had the good fortune to be the holder of Harvard University's Peter Brooks Saltonstall Scholarship and I should like to express my sincere thanks to the administrators of Harvard University for making it possible. I am also greatly indebted to the administrators of the U. S. Educational Foundation who awarded me a Fulbright Travel Grant to and from the United States. The American Museum of Natural History provided extensive facilities for carrying out taxonomic work on its collection of Australian, New Guinea, and Pacific Island birds, easily the world's finest. In addition, they were kind enough to provide a grant from the Frank M. Chapman Fund to help defray the costs of living in New York.

Dr. Ernst Mayr, my supervisor at Harvard, directed my work. The approach and method of analysis were suggested by him and many of the ideas were developed in discussions with him or from his published work. I cannot thank him too much for his interest, encouragement, and great inspiration.

Additional field work has been carried out in Australia in the period 1955-1959. The costs of this were mostly borne by the Trustees of the Australian Museum. The Trustees of the Science and Industry Endowment Fund of the Australian Commonwealth Scientific and Industrial Research Organization were, however, kind enough to make me a grant to carry out my 1959 field work in Western Australia. Transport in central Australia in 1958 was kindly made available by the Director, and Mr. Alan Newsome, of the Animal Industry Division of the Northern Territory Administration. Dr. W. D. L. Ride, Director of the Western Australian Museum, Perth, kindly arranged for me to join his field party to the Barlee Range in 1959.

A very special debt is owing to the Trustees and ornithologists of the many museums I visited in order to carry out taxonomic work or to check on outstanding matters: Museum of Comparative Zoology, Harvard; American Museum of Natural History,

New York; Academy of Natural Sciences, Philadelphia; Los Angeles County Museum; British Museum (Nat. Hist.), London; National Museum of Victoria, Melbourne; South Australian Museum, Adelaide. The bulk of the later work was, of course, carried out at the Australian Museum, Sydney. From time to time I have been able to discuss aspects of the work with many people and to test conclusions derived from bird studies against other animal groups.

The following biologists were kind enough to read the manuscript and make numerous helpful suggestions: Dr. E. Mayr, Dr. D. L. Serventy, Prof. R. Crocker, and Dr. D. Amadon. To these I should also like to express a debt of gratitude.

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Table 1

THE MAJOR VEGETATION FORMATIONS OCCURRING IN AUSTRALIA: THEIR CHARACTERISTICS

(Modified and enlarged from that in Wood (1949))

FORMATION	CHARACTERISTICS
Rain Forest	Dense assemblage of trees, canopy continuous, woody climbers (vines) present. Monsoon or pseudo rain forest, narrow strips of dense soft woods along the banks of rivers in parts of the northern coastal region, have a somewhat similar consistency.
Sclerophyll Forest	Trees of forest form, in closed community; dense undergrowth of hard leaved shrubs; grass rare. (Map groups wet and dry sclerophyll.)
Savannah Woodland	Rather open parklike communities of trees, with scattered shrubs and a few herbs. Grassy underfoot and with open areas.
Savannah Grassland	Grasslands with herbs and a few sub-fruticose shrubs, interspersed with a few trees, or small clumps of trees. Sometimes intermixed with tracts of savannah woodland.
Mallee Scrub	Associations of dwarf eucalypts, the trees characterised by multiple stems arising from a common base; growing in semi-arid regions frequently on soil with characteristic qualities (mallee soil). Growth is generally rather open. Scattered shrubs and tracts of clumped porcupine grass (*Triodia*) are present.
Mulga Scrub (desert steppe)	Small trees with dense or scattered shrubs, few herbs, and with vast tracts dominated by the Mulga (*Acacia ancura*).
Desert Grassland (desert steppe)	Sand-plain covered with tussocks and clumps of spiny sclerophyllous grass (sometimes fairly continuous, sometimes sparse), mainly spinifex or porcupine grass (*Triodia*). Chenopodaceous plants. Marked seasonal herbage after rains. Gibber desert, plains with gravel and stone pavement, vegetation minimal, is included here.
Mangroves	Shrubs or trees in littoral zone, growing in formations that may be relatively open or of dense and shady consistency.
Swamps, marshes and rivers	Areas of fresh water that are either open, associated with sparse trees, or densely covered with reed-bed.
Miscellaneous	Includes various minor subdivisions, e.g. rocky outcrops and river gorges.

TABLE 2

MAJOR VEGETATION FORMATION: AREA COVERED BY EACH, AND RICHNESS IN TERMS OF NUMBER OF BIRD SPECIES

Each bird species is included only once, it being placed under the formation to which it is confined or, in the case of those species that occur in more than one, under the formation that is judged to be its main habitat.

Type	HABITAT		BIRD SPECIES		
	Area in sq. miles	% of continental area	(Approx.) Number of species	% of total avifauna	Number of sq. miles of habitat/species
Rain forest	20,000	0.66%	81	16	247 (x)
Sclerophyll forest	210,000	7	86	16	2,500
Savannah woodland	720,000	24	? (148)	(28)	4,932
Savannah grassland	480,000	16	? (59)	(11.5)	8,135
Mallee	210,000	7	10	2	23,330
Mulga	900,000	30	? (24)	(4.5)	37,500
Desert grassland (spinifex) and steppe & gibber	420,000	14	17	3	24,705
Mangroves	Negligible (perhaps 1,000 sq.m.)	Negligible	16	3	70
Swamps & marshes	Negligible	Negligible	74	14	—
Miscellaneous	Negligible	Negligible	16	2.5	—
TOTAL (actual)	2,984,000		531	—	5,772

(x) A high proportion of the species confined to this habitat are New Guinea species that have colonized the continent in comparatively recent times.

TABLE 3

AUSTRALIAN BIRD SPECIES: SUMMARY OF GEOGRAPHIC VARIATION, ISOLATION AND SPECIATION TRENDS

In the column referring to the number of isolates beyond Australia the symbol "x" means that there is a solitary differentiated population beyond the continent, and "(x)" means that the species extends there without differentiation. In order to enable proper comparisons to be made, each species extending beyond the continent is regarded as having a "parental form" both inside and outside of the continent. That is to say, the "x"'s in this particular column are not included in the totals and subsequent calculations. All figures refer only to isolates in the section to the *east* of Wallace's Line.

In the sixth column, if the species is a member of a superspecies group centred to the *west* of Wallace's Line this is indicated by the symbol (or figure) being placed in brackets. Again these are not included in the totals.

TABLE 3 (Continued)

	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differentiation	Slight Diffn.	
		Fam: PODICIPITIDAE						
Podiceps cristatus	x			(x)				
P. novae-hollandiae		x		2	(x)			
P. poliocephalus		x						
		Fam: ACCIPITRIDAE						
Elanus notatus	x							
E. scriptus	x				(x)			
Aviceda suberistata			1?	12	(x)		1	
Milvus migrans	x			(x)	(x)			
Lophoictinia isura	x							
Hamirostra melanosternon	x							
Haliastur sphenurus	x							
H. indus	x							
Accipiter fasciatus		x		6				x
A. cirrhocephalus		x		3				x
A. novae-hollandiae		x		19				
Erythrotriorchis radiatus	x							
Hieraaetus morphnoides	x			x	(x)			
Aquila audax			1	(x)	(x)		1	
Haliaeetus leucogaster	x			(x)				
Circus approximans	x			(x)				
C. assimilis	x							
Falco hypoleucos	x							
Falco subniger	x							

F. berigora		x		x	(x)			
F. peregrinus			1?	2	Cosmop		1	
F. longipennis		x			(x)			
F. cenchroides	x			1	(x)			
Pandion haliaetus		x		(x)	Cosmop			1
		Fam: GRUIDAE						
Grus rubicunda	x				(x)			
		Fam: ARDEIDAE						
Ardea sumatrana	x				(x)			
Egretta garzetta	x			x	(x)			
E. intermedia	x			x	(x)			
E. alba	x			1-2?	Cosmop			
Notophoyx novae-hollandiae	x			x				
Ardea pacifica	x			(x)				
N. picata	x			(x)				
Demigretta sacra	x			x				
Nycticorax caledonicus	x			3				
Butorides striatus			5	8	(x)	1	4	
Ixobrychus minutus	x			1	(x)			
Dupetor flavicollis	x			2	(x)			
Botaurus stellaris	x			(x)	(x)			
	Fam: THRESKIORNITHIDAE							
Plegadis falcinellus	x			(x)	Cosmop			
Threskiornis aethiopica		x		(x)	(x)			
Carphibis spinicollis	x							
Platalea leucorodia regia	x			(x)	(x)			
P. flavipes	x							
		Fam: CICONIIDAE						
Xenorhynchus asiaticus	x			(x)	(x)			

TABLE 3 (Continued)

Species	MONOTYPIC (in Aust.)	POLYTYPIC				ISOLATES		HYBRID ZONES
	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differ-entia-tion	Slight Diffn.	
Fam: ANATIDAE								
Cereopsis novaehollandiae	x							
Anseranas semipalmata	x			(x)				
Cheniscus coromandelianus	x			(x)				
C. pulchellus	x			(x)				
Chenonetta jubata	x			(x)				
Chenopis atrata	x			(x)				
Dendrocygna arcuata	x			2	(x)			
D. eytoni	x			(x)				
Tadorna radjah	x			(x)	(x)			
Casarca tadornoides	x							
Anas superciliosa	x			1	(x)			
A. castanea	x			2				
A. gibberifrons	x			2	x			
Spatula rhynchotis	x			(x)	(x)			
Malacorhynchus membranaceus	x							
Stictonetta naevosa	x							
Aythya australis	x			x)				
Oxyura australis	x							
Biziura lobata	x							

		Fam: RALLIDAE					
Rallus pectoralis			1	2-3			1
Rallus philippensis			1	18			1
Eulabeornis castaneoventris	x			x			
Rallina tricolor	x			3			
Porzana fluminea			1				1
P. pusilla	x			x	(x)		
P. tabuensis	x		1	6	x		1
Poliolimnas cinereus	x			6			
Amaurornis olivacea	x			2-3			
Tribonyx mortieri	x						
T. ventralis	x						
Gallinula tenebrosa			1	2	(x)		1
Porphyrio porphyrio			2	8	(x)	1	1
Fulica atra	x				(x)		
		Fam: TURNICIDAE					
Turnix maculosa		x		1-2			
T. varia			3	x			3
T. castanota			1			1	
T. melanogaster	x						
T. velox		x					
T. pyrrhothorax			1!			1	
Pedionomus torquatus	x						
		Fam: COLUMBIDAE					
Ptilinopus regina			1	2-3	x	1	
P. superbus	x			(x)			
P. alligator	x				x		
Megaloprepia magnifica			2	2			2
Ducula spilorrhoa	x			1	x		
Lopholaimus							

TABLE 3 (Continued)

	MONOTYPIC (In Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differentiation	Slight Diffn.	
antarcticus		x						
Columba norfolciensis		x						
Macropygia phasianella			1	x	x		1	
Geopelia striata			1	3			1	1
G. cuneata		x						
G. humeralis		x		x				
Chalcophaps indica			1	4			1	
Phaps chalcoptera		x						
P. elegans		x						
Histriophaps histrionica	x							
Petrophassa albipennis	x				x			
P. rufipennis	x				x			
Geophaps scripta		x			x			
G. smithi	x				x			
Lophophaps plumifera			3-4			1	2-3	
Ocyphaps lophotes			1				1	1?
Leucosarcia melanoleuca		x						
Fam: PSITTACIDAE								
Trichoglossus moluccanus			1		x	1		
Opopsitta diophthalma			2	3		2		
Probosciger								

aterrimus	x			3				
Kakatoe roseicapilla		x						
Leptolophus hollandicus	x							
Larius roratus	x			6				
Geoffroyus geoffroyi	x			12				
Polytelis swainsoni	x							
P. alexandrae	x							
Platycercus elegans			2		x	1	1	H. with flaviolus
Platycercus flaveolus		x			x			3
P. caledonicus	x				x			
P. adscitus			1-2				1-2	1
P. venustus		x			x			
P. eximius			1		x		1	1
P. icterotis		x			x			
Purpureicephalus spurius	x							
Barnadius barnardi			1		x	1		1
Barnardius zonarius			3		x	1	2	1
Psephotus haematonotus		x						
P. varius			1		x		1	
P. haematogaster			2			1	1	
P. pulcherrimus	x				x			
P. chrysopterygius			1		x	1		
Neophema pulchella	x				x			
N. splendida		x			x			
N. bourki	x							
N. chrysogaster	x							
N. chrysostoma	x							

TABLE 3 (Continued)

	MONOTYPIC (in Aust.)	POLYTYPIC			ISOLATES			HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differ-entia-tion	Slight Diffn.	
N. elegans			1				1	
N. petrophila			1				1	
Lathamus discolor	x							
Melopsittacus undulatus	x							
Fam: CORACIIDAE								
Eurystomus orientalis	x			x				
Fam: ALCEDINIDAE								
Alcyone azurea			1	1-2			1	
A. pusilla				1				1
Syma torotoro	x			3				
Dacelo novae-guineae			1?				1	
D. leachii			1	x			1	1?
Halcyon macleayi			1	1-2			1	
H. pyrrhopygius	x							
H. sanctus		x		3-4	x			
H. chloris		x		27	x			
Tanysiptera sylvia	x			x				
Fam: MEROPIDAE								
Merops ornatus	x							
Fam: MENURIDAE								
Menura novae-hollandiae			1?			1		
M. alberti	x							
Fam: ATRICHORNITHIDAE								
Atrichornis rufescens	x				x }			
A. clamosus	x				x }			

Fam: CAMPEPHAGIDAE							
Pteropodocys maxima	x						
Coracina novaehollandiae			2	2-3	x		2
C. papuensis			2	9			2
C. robusta		x					
C. lineata	x			10			
C. tenuirostris			1	18			1
Lalage sueurii tricolor	x			x	x		
L. leucomela			2	9	x		2
Fam: MUSCICAPIDAE Sub-fam: MUSCICAPINAE							
Rhipidura fuliginosa			5	7	x	1	4
R. rufifrons			1	20-21	x	1	
R. rufiventris		x		11	x		
R. leucophrys		x		1			
Seisura inquieta			2			1	1
Piezorhynchus alecto			2	3		1	1
Myiagra rubecula		x	1	1			1
M. cyanoleuca	x			(x)			
M. ruficollis	x			x			
Machaerirhynchus flaviventer			1	2			1
Arses kaupi	x				x		
Arses telescopthalmus	x			3	x		
Monarcha melanopsis		x		x	x		
M. frater	x			2	x		
M. trivirgata			1	10		1	
M. leucotis	x						
Microeca leucophaea			1	x			1

TABLE 3 (Continued)

Species	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differ-entia-tion	Slight Diffn.	
Microeca flavigaster			1	1			1	
M. brunneicauda	x				x			
M. griseoceps	x			2				
Petroica multicolor			1	12			1	
P. goodenovii		x						
P. phoenicea	x							
P. rosea	x				x			
P. rodinogaster	x							
P. cucullata		x			x			
P. vittata	x				x			
Eopsaltria australis			2			1	1	
E. georgiana	x							
Peneoenanthe pulverulenta		x		x				
Heteromyias cinereifrons	x				x			
Poecilodryas superciliosa			1			1		
Tregellasia capito			1		x		1	
T. leucops	x			6	x			
Tribe: PACHYCEPHALINI								
Pachycephala pectoralis			5-7	51+		2	3-5	
P. rufiventris		x		2				
P. rufogularis	x							
P. inornata			1				1	
P. lanioides			3			1	2	
P. olivacea			1?				1	

P. simplex			1	4		1	
Falcunculus frontatus			2			2	
Oreoica gutturalis		x					
Sub-fam: TIMALIINAE Tribe: CINCLOSOMATINI							
Sphenostoma cristatum		x					
Psophodes olivaceus		x			x		
P. nigrogularis			1		x		
Drymodes brunneopygia		x					1
D. superciliaris			1	2			1
Orthonyx temmincki	x			2			
O. spaldingi	x						
Sub-fam: SYLVIINAE							
Megalurus gramineus			2	x			2
M. timorensis	x			3-4			
Acrocephalus stentorius			1-2	1	(x)		1-2
Sub-fam: MALURINAE							
Epthianura albifrons			1				1
E. tricolor	x						
E. aurifrons	x						
E. crocea			3			3	
Ashbyia lovensis	x						
Gerygone olivacea			2	x		1	1
G. richmondi			2		x		2
G. palpebrosa			2	1-2		1	1
G. magnirostris-tenebrosa			1	7		1	
G. chloronota	x			1			
Gerygone							

TABLE 3 (Continued)

Species	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differ-entia-tion	Slight Diffn.	
levigaster			2		x		2	
G. cantator	x				x			
G. fusca		x		1	x			
Smicrornis brevirostris		x						
Aphelocephala leucopsis			2				2	
A. pectoralis	x							
A. nigricincta	x							
Acanthiza lineata			1-2				1-2	
A. nana			2?				2	
A. inornata		x						
A. ewingi	x							
A. pusilla			4?			1	1	
A. robustirostris	x						4	
A. uropygialis		x						
A. iredalei			2					
A. reguloides			2?			1	1	
A. chrysorrhoa			2				2	
Acanthornis magnus	x							
Sericornis frontalis			1		x		1	1
S. maculata			3		x		3	1
S. humilis	x				x			
S. beccarii	x			7	x			
S. lathami			1				1	
S. magnirostris			1				1	
Oreoscopus gutturalis	x							
Pyrrholaemus								

brunneus	x						
Hylacola pyrrhopygia		x					
H. cauta			2			2	
Calamanthus fuliginosus			2	x		2	1
C. campestris			1	x		1	
Chthonicola sagittata		x					
Origma rubricata	x						
Pycnoptilus floccosus		x					
Eremiornis carteri	x						
Cinclorhamphus cruralis		x					
C. mathewsi		x					
Amytornis textilis			3	x	1	2	
A. modestus			1	x		1	
A. goyderi	x			x			
A. striatus			2	x	1	1	
A. woodwardi	x			x			
A. dorotheae	x			x			
A. housei	x			x			
Dasyornis brachypterus			1		1		
D. broadbenti			2		1	1	
Stipiturus malachurus			6	x	1	5	
S. ruficeps	x			x			
Malurus cyaneus			2	x		2	1
Malurus melanotus	x			x			
M. callainus		x		x			
M. splendens				x			
M. leucopterus			1		1		
M. lamberti			1	x		1	2
M. elegans	x			x			

TABLE 3 (Continued)

Species	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differentiation	Slight Diffn.	
M. amabilis	x				x			
M. dulcis	x				x			
M. pulcherrimus			1		x		1	
M. melanocephalus			1				1	
M. coronata			1				1	
Fam: ARTAMIDAE								
Artamus leucorhynchus		x		7	x			
A. personatus	x							
A. superciliosus	x							
A. cinereus		x		1				
A. cyanopterus		x						
A. minor		x						
Fam: SITTIDAE								
Neositta chrysoptera			3	3	x		3	3?
Climacteris picumnus		x			x			
C. rufa			1		x		1	
C. melanura			1		x	1		
C. leucophaea			2	3	x	1	1	
C. erythrops		x			x			
C. affinis		x			x			
Fam: DICAEIDAE								
Dicaeum hirundinaceum		x		2-3	x			
Pardalotus punctatus			2		x		2	
P. xanthopygus	x				x			
P. quadragintus	x				x			
P. striatus		x						

P. substriatus		x						
P. melanocephalus			1-2				1-2	?1
P. rubricatus		x						
Fam: NECTARINIIDAE								
Nectarinaria jugularis	x			7				
Fam: MELIPHAGINAE								
Melithreptus lunatus			1		x	1		
M. affinis	x				x			
M. albogularis		x		(x)				
M. brevirostris		x						
M. gularis		x			x			1
M. validirostris	x				x			
Plectorhyncha lanceolata		x						
Myzomela dibapha		x		7	x			
M. erythrocephala			1	1	x	1		
M. pectoralis	x							
M. nigra	x							
M. obscura			1	5			1	
Certhionyx variegatus	x							
Acanthorhynchus tenuirostris			2		x		2	
A. superciliosus	x				x			
Gliciphila melanops		x						
Ramsayornis modesta	x			(x)				
R. fasciata		x						
Lichmera indistincta		x		5				
Grantiella picta	x							
Conopophila whitei	x							

TABLE 3 (Continued)

	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differ-entia-tion	Slight Diffn.	
C. albogularis	x			x				
C. rufogularis	x							
Zanthomiza phrygia		x						
Glycichaera fallax	x			1-2				
Meliphaga lewini		x						
M. notata			1		x		1	
M. albilineata	x							
M. virescens		x			x			
M. versicolor	x			2	x			
M. fasciogularis	x							
M. frenata	x							
M. gracilis			1	1			1	
M. fusca		x						
M. chrysops		x						
M. flavicollis	x				x			
M. leucotis		x			x			
M. cassidix	x				x			
Meliphaga melanops		x			x			
M. cratitia		x						
M. keartlandi		x						
M. ornata		x						
M. plumula		x						
M. flavescens			2	x			2	
M. penicillata		x						
M. flava		x						
M. macleayana	x				x			
M. chrysotis	x			5	x			
Trichodere cockerelli	x							

Stomiopera unicolor		x						
Phylidonyris pyrrhoptera			2				2	
P. novae-hollandiae			1				1	
P. niger			1				1	
P. albifrons	x							
Manorina melanophrys		x						
Myzantha melanocephala		x						
M. flavigula		x			x }			
M. melanotis	x				x }			
Anthochaera chrysoptera			2			1	1	
A. carunculata			1		x }		1	
A. paradoxa	x				x }			
Acanthagenys rufogularis		x						
Entomyzon cyanotis			1	x		1		
Philemon novae-guineae			1	8+		1		
P. argenticeps		x						
P. corniculatus		x		x				
P. citreogularis		x		x				
Fam: ZOSTEROPIDAE								
Zosterops lateralis			3	6			3	2
Z. lutea			2		x		2	
Fam: PLOCEIDAE Sub-fam: ESTRILDINAE								
Estrilda temporalis			2				2	1
Zonaeginthus pictus	x							

TABLE 3 (Continued)

	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
Species	Variation nil.	Clinal Varn. only	No. of Isol. in Aust.	No. of Isol. beyond Aust.	Member of Super-species	Marked to mod. Differ-entia-tion	Slight Diffn.	
Z. bellus	x				x			
Z. oculatus	x				x			
Z. guttatus	x							
Poephila guttata		x		2				
P. bichenovii		x						1
P. phaeton			1	1		1		
P. ruficauda			1?				1	
P. cincta			former isol.		x			1
P. acuticauda		x			x			
P. personata			1			1		
Poephila gouldiae		x						
Erythrura trichroa	x			8	x			
Lonchura pectoralis	x							
L. modesta	x							
L. castaneothorax			?1	1	x		1	
L. flaviprymna	x				x			
Fam: ORIOLIDAE								
Oriolus sagittatus			1	x	x	1		
O. flavocinctus		x		x	x			
Sphecotheres vieilloti			1?	x			1	x
S. flaviventris		x		x				
Fam: DICRURIDAE								
Chibia bracteata	x			6				
Fam: EULABETIDAE								
Aplonis metallica	x			3				
Fam: CRACTICIDAE								

Strepera graculina				1		x	1		
S. fuliginosa		x				x			
S. versicolor				5		x	2	3	
S. arguta		x				x			
Cracticus nigrogularis			x						
C. quoyi				1	1			1	
C. torquatus				2			1	1	
C. mentalis		x			(x)				
Gymnorhina tibicen				1	x	x		1	
G. dorsalis		x				x			1
G. hypoleuca				1		x		1	
Fam: GRALLINIDAE Sub-fam: GRALLINAE									
Grallina cyanoleuca		x							
Sub-fam: CORCORACINAE									
Corcorax melanorhamphus		x							
Struthidea cinerea		x							
Fam: PTILONORHYNCHIDAE									
Ailuroedus crassirostris				1	4-5		1		
Scenopoeetes dentirostris		x							
Ptilonorhynchus violaceus				1			1		
Chlamydera maculata				1			1		
C. cerviniventris		x			(x)				
C. nuchalis			x with step						1
Sericulus chrysocephalus			x						
Prionodura newtoniana		x							
TOTAL:	425	190	99	213-220	487-502	125(29)	59	154-161	33

TABLE 4
AUSTRALIAN BIRD FAMILIES: SUMMARY OF GEOGRAPHIC VARIATION, ISOLATION AND SPECIATION

FAMILY	MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
	Variation nil	Clinical Varn. only	Number of isolates in Aust.	Number isol. beyond Aust. (est.)	Member of Super-species	Marked to mod. Diffn.	Slight Diffn.	
Podicipitidae 3, (3)	1	2		2	(1)			
Accipitridae, Falconidae, and Pandionidae 24, (24)	15	6	3	43	(8)		3	3
Gruidae 1, (1)	1				(1)			
Ardeidae 13, (13)	12		5	15-16	(7)	1	4	
Threskiornithidae 5, (5)	4	1			(2)			
Ciconiidae 1, (1)	1				(1)			
Anatidae 19, (19)	19			7				
Rallidae 14, (14)	9		7	47-49		1	6	
Turnicidae 7, (7)	2	2	5	1-2		2	3	
Columbidae 22, (22)	7	8	10-11	12-13	8	2	8-9	2
Psittacidae 30, (52)	15	6	17-18	24	14	8	9-10	8
Coraciidae 1, (1)	1							
Alcedinidae 10, (10)	3	2	4	36-39	2		4	2
Meropidae 1, (1)	1							
Menuridae 2, (2)	1		1			1		
Atrichornithidae 2, (2)	2				2			
Campephagidae 8, (8)	3	1	7	48-49	3		7	
Muscicapidae								
Muscicapinae 43, (47)	16	9	33-35	138-139	14	13	20-22	
Timaliinae 7, (10)	2	3	2	4	2		2	
Sylviinae 3, (5)	1		3-4	4-5	(1)		3-4	
Malurinae 69, (69)	25	10	61-62	17-18	28	14	47-48	5
Artamidae 6, (6)	2	4		8	1			

FAMILY	MONOTYPIC (in Aust.)		POLYTYPIC		ISOLATES			HYBRID ZONES
	Variation nil	Clinical Varn. only	Number of Isolates in Aust.	Number isol. beyond Aust. (est.)	Member of Super-species	Marked to mod. Diffn.	Slight Diffn.	
Sittidae 7, (7)		3	7	6	7	2	5	3
Dicaeidae 8, (8)	2	4	3-4	2-3	4		3-4	1
Nectariniidae 1, (1)	1			7				
Meliphagidae 67, (67)	24	29	18	35-36	21	5	13	1
Zosteropidae 2, (2)			5	6	1		5	2
Ploceidae Estrildinae 18, (18)	8	4	6	12	7	2	4	3
Oriolidae 4, (4)		2	2		2	1	1	1
Dicruridae 1, (1)	1			6				
Eulabetidae 1, (1)	1			3				
Cracticidae 11, (11)	4	1	11	1	7	4	7	1
Grallinidae 3, (3)	3							
Ptilonorhynchidae 8, (8)	3	2	3	4-5		3		1
TOTAL 425	190	99	213-220	487-502	125(29)	59	154-161	33

The figures in the first column indicate the sample used in the present study, those in brackets the total number of species in each family in Australia. In addition, the following families and subfamilies of breeding land and fresh-water birds occur in Australia: Casuaridae, 1 species; Dromaeidae, 1; Phalacrocopacidae, 5, one of which is marine; Pelecanidae, 1; Megapodiidae, 3; Phasionidae, 3; Cuculidae, 11; Otidae, 1; Burtinidae, 1; Jacanidae, 1; Himantopidae, 2; Charadriidae, 5 (plus visitors); Glariolidae, 1; Recurvirostridae, 3; Scolopaciidae, 1; Laridae, 2, plus many marine species; Strigidae, 8; Aegothelidae, 1; Podargidae, 3; Caprimulgidae, 3; Apodidae, 1 (plus 2 migrants); Pittidae, 3; Alaudidae, 1; Hirundinidae, 4; Turdinae, 1; Corvidae, 3; Paradisaeidae, 3.

The figures in brackets in the sixth column refer to the number of species belonging to superspecies groups centered to the *west* of Wallace's Line.

TABLE 5
THE INFLUENCE OF VEGETATION FORMATION ON SPECIATION. ABSOLUTE FIGURES

HABITAT		MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYRID ZONES
	Number of species in sample	Variation nil	Clinal varn. only	Number of isolates in Aust.	Number isol. beyond Aust. (est.)	Member of Super-species	Marked to mod. Differentiation	Slight Diffn.	
Rain Forest	70	34	9	31	177-183	20	13	18	—
Sclerophyll Forest	80	28	14	71-72	102-103	30 (1)	14	57-58	8
Savannah Woodland	113	32	43	61-64	91-95	32 (3)	19	42-45	18
Savannah Grassland	43	20	16	10	4	8 (4)	3	7	5
Mallee	10	5	2	4		4		4	
Mulga	15	7	8		1	2			
Desert Grassland (Spinifex)	15	9	1	8		10	3	5	1
Mangroves	16	8	2	10-11	52	13	2	8-9	1
Swamps	54	43	3	11-12	59-63	2 (20)	1	10-11	
Miscell. Habitats	9	4	1	7-8	1	4 (1)	4	3-4	
TOTAL:	425	190	99	213-220	487-502	125 (29)	59	154-161	33

In the seventh column the figures in brackets refer to the numbers of species belonging to superspecies groups centered to the *west* of Wallace's Line.

TABLE 6
THE INFLUENCE OF VEGETATION FORMATION ON SPECIATION. FIGURES EXPRESSED IN TERMS OF PERCENTAGES

HABITAT	MONOTYPIC (in Aust)		POLYTYPIC				ISOLATES		HYBRID ZONES
	Number of Species	Variation nil	Clinal Varn. only	Number of isolates in Aust.	Number isol. beyond Aust. (est.)	Member of Super-species	Marked to mod. Differ-entia-tion	Slight Diffn.	
Rain Forest	15	18	9.1	14	35.8	16	22	11.3	
Sclerophyll Forest	20	14.7	14.1	33.1	20.8	24	25	37.2	24
Savannah Woodland	28	17	43.1	30	18.8	25.6	32	28.4	54
Savannah Grassland	10	10.5	16.1	4.7	1	6.4	5	4.2	16
Mallee	2	2.6	2.1	1.7		3.2		2.4	
Mulga	3.4	3.7	8.1		.5	1.6			
Desert Grassland (Spinifex)	3.4	4.7	1.1	3.5		8	5	3.1	3
Mangroves	3.6	4.2	2.1	4.8	10.5	10.4	3	5	3
Swamps	12.5	22.6	3.1	5.1	12.4	1.6	1.4	6.2	
Miscell. Habitats	2.0	2	1.1	3.1	.5	3.2	6.6	2.2	
TOTAL:	100	100	100	100	100	100	100	100	100

TABLE 7

THE INFLUENCE OF SEASONAL MOVEMENTS ON SPECIATION

		MONOTYPIC (in Aust.)		POLYTYPIC			ISOLATES		HYBRID ZONES
Category		Variation nil.	Clinical Varn. only	No. of isol. in Aust.	No. of isol. beyond Aust.	Member of Super-species	Marked to mod. Diffn.	Slight Diffn.	
Sedentary species	(294)	111	65	191-196	286-293	105 (10)	49	143-149	30
South-north migrants	(32)	10	11	15-17	119-125	10 (1)	5	9-10	—
Nomadic species	(99)	69	23	7	82-84	10 (18)	5	2	3
TOTAL:	425	190	99	213-220	487-502	125 (29)	59	154-161	33

In the sixth column the figures in brackets refer to the numbers of species belonging to superspecies groups centered to the *west* of Wallace's Line.

TABLE 8
ISOLATION AND SPECIATION ON OFFSHORE ISLANDS

Island	Distance offshore (miles)	Morphologically Distinctive Isolates
Tasmania (southeastern)	130. Longest water gap. 50	About 12 that have reached or are approaching the degree of differentiation typical of species, plus 20 lesser isolates.
King Island (southeastern)	50 from Tasm. 50 from Vict.	Minor forms of Melithreptus gularis, M. affinis, Acanthorynchus tenuirostris, Acanthiza ewingi, Malurus cyaneus (also on Flinders Island). Total: about 5.
Kangaroo Island (southern)	5-10	Minor forms of Melithreptus atricapillus, Anthochaera chrysoptera, Phylidonyris pyrrhoptera, Meliornis novaehollandiae, Acanthorhynchus tenuirostris, Meliphaga leucotis, Estrilda temporalis, Acanthiza pusilla, Stipiturus malachurus, Zonaeginthus bellus. Total: about 10.
Recherche Archipelago (southwestern)	5-20	Minor form of Sericornis maculata.
Abrolhos Islands (western)	40	Minor forms of Turnix varia, Sericornis maculata.
Dirk Hartog Island (western)	24	Malurus leucopterus (also on Barrow Is.). Minor forms of Calamanthus fuliginosus, Stipiturus malachurus.
Barrow Island (western)	35	Eremiornis carteri (minor form). An insular race of Anthus australis has been described from here.
Bernier Island (western)	20	Malurus lamberti minor form.
Melville Island (northwestern)	20	Minor forms of Turnix castanota (?), Coracina papuensis, Dacelo leachii, Meliphaga flavescens, Entomyzon cyanotis, Philemon novaeguineae, Myzomela obscura (?). Total: about 7.
Capricorn Islands (eastern)	25	Minor form of Zosterops lateralis.

TABLE 9

AVIFAUNAL RELATIONSHIPS BETWEEN AUSTRALIA AND THE MORE REMOTE SURROUNDING ISLANDS

	Species that have colonized Australia	Australian species that have colonized island
New Zealand	nil	8-10 in recent times (Falla, 1953), plus many older elements (Meliphagidae, Muscicapinae).
Lord Howe Island	nil	Up to about 10 (see Hindwood, 1940).
New Caledonia	nil	About 18 (see Mayr, 1945a).
Timor	20-22 (Mayr, 1944b)	About 17 (Mayr, 1944b).
New Guinea	66 plus	92 plus.

TABLE 10

CONTINENTAL AND ARCHIPELAGO SPECIATION. COMPARISON OF NUMBER OF MORPHOLOGICALLY DIFFERENTIATED ISOLATES IN BIRD SPECIES COMMON TO BOTH AREAS

Species	Number of Morphologically differentiated Isolates in southwest Pacific (Fig. 28)	Number of Isolates in Australia
Podiceps novae-hollandiae	2	—
Aviceda subcristata	4	1
Haliastur sphenurus	—	—
Haliastur indus	—	—
Accipiter novae-hollandiae	9	—
Accipiter fasciatus	—	—
Circus approximans	—	—
Falco peregrinus	1	—
Pandion haliaetus	1	—
Notophoyx novaehollandiae	—	—
Demigretta sacra	1	—
Nycticorax caledonicus	2	—
Butorides striatus	4	5
Dupetor flavicollis	1	—
Botaurus stellaris	—	—
Dendrocygna arcuata	1	—
Anas superciliosa	1	—
A gibberifrons	1	—
Aythya australis	—	—
Rallus philippensis	12	1
Rallina tricolor	2	—
Porzana tabuensis	—	1
Poliolimnas cinereus	4	—
Amaurornis olivaceus	1	—
Porphyrio porphyrio	5	2
Turnix maculosa	1	—

TABLE 10 (Continued)

Species	Number of Morphologically differentiated Isolates in southwest Pacific (Fig. 28)	Number of Isolates in Australia
Turnix varia	—	3
Chalcophaps indica	1	1
Trichoglossus haematodus	2	1
Eurystomus orientalis	—	—
Halcyon sanctus	2	—
Halcyon chloris	26	—
Coracina lineata	6	—
C. papuensis	5	2-3
C. tenuirostris	10	1
Lalage leucomela	5	2-3
Rhipidura rufifrons	18	1
R. leucophrys	1	—
R. fuliginosa	2	4-5
R. rufiventris	5	—
Piezorhynchus alecto	1	2
Petroica multicolor	10	1
Pachycephala pectoralis	34	5-7
P. rufiventris	1	—
Artamus leucorhynchus	4	—
Nectarinaria jugularis	1	—
Myzomela dibapha	—	—
Lichmera indistincta	1	—
Philemon novaeguineae	1	1
Zosterops lateralis	6	6
Erythrura trichroa	4	—
Chibia bracteata	2	—
Aplonis metallica	1	—
TOTAL	201	38-43

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THE SPITSBERGEN ARCTOCERATIDS

By Bernhard Kummel

WITH NINE PLATES

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No. 9 — *The Spitsbergen Arctoceratids*

By Bernhard Kummel

The most characteristic ammonoids of the Lower Triassic deposits of Spitsbergen are species of the genus *Arctoceras*. Lindström (1865), Oberg (1877), and Mojsisovics (1886) together have described 7 species (under the genus *Ceratites*) that have been assigned to *Arctoceras* since Hyatt (1900, p. 559) established the genus designating *Ceratites polaris* as the type. The species of *Arctoceras* from Spitsbergen are as follows:

A. blomstrandi (Lindström)
A. simplex (Mojsisovics)
A. polare (Mojsisovics)
A. whitei (Mojsisovics)
A. öbergi (Mojsisovics)
A. lindströmi (Mojsisovics)
A. costatus (Oberg)

The specimens upon which these species were based came from the *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen. Spath (1921, 1934) had opportunity to study additional large collections from the same horizon at a number of different localities and accepted all of the species previously described even though he clearly recognized the presence of numerous transitions between all of the species. Frebold (1930) likewise studied specimens of this genus from Spitsbergen and accepted all of the species then known.

Between the time of the original description of these species by Lindström, Öberg, and Mojsisovics and the later studies by Frebold and Spath, there was published a most interesting commentary on the Spitsbergen arctoceratids by Wepfer (1912, p. 7, footnote) which reads as follows: "E. v. Mojsisovics hat in den 'arktischen Triasfaunen' 32 Ceratiten aus den Poisdonienschichten von Spitzbergen beschrieben unter den teilweise neuen Namen *simplex*, *Whitei*, *Blomstrandi* (Lindström), *polaris*, *costatus*, *Oebergi*, *Lindströmi*, die allesamt zu einem und demselben Typhus gehören, nämlich zu der 'Untergruppe des *Cer. polaris*.' In der Tat stehen sie sich alle sehr nahe und die Unterscheidung in sieben getrennte Spezies beruht auf recht subtilen Unterschieden. Immerhin könnte man sie gelten lassen, wenn man annehmen dürfte, dass diese 32 Stücke die Vollständigkeit der in den Posidonienschichten vorkommenden Fauna darstellen würden. Das wird aber kaum jemand behaupten wollen, wenn er in Betracht zieht, dass auf der Spitzbergener Exkursion des internationalen Geologenkongresses (an der ich teilgenommen habe) jeder Teilnehmer Dutzende von gut erhaltenen Ceratiten aus den betreffenden Schichten sammeln konnte. Ich habe z. B. über 30 Stück gesammelt; schon diese 30 nach Mojsisovics' Arbeit bestimmen zu wollen, stösst auf die grössten Schwierigkeiten, denn so und so viele Exemplare stehen in der und jener Beziehung zwischen zwei 'Spezies' and füllen somit eine (bisher künstliche) Lücke teilweise aus. — Als unbefangener Beobachter kann man nur feststellen, dass diese Ceratiten samt und sonders zu einem Typhus gehören, zu dem des *Ceratites polaris* E. v. Mojs. oder — wenn man der Priortät den Vorrang vor gänzlich unzulänglichen Figuren geben will — dem des *Cer. Bloemstrandi* Lindstr. Es ist stets tief zu bedauern, wenn eine Fauna beschrieben wird, solange ungenügende Aufsammlungen gemacht worden sind; hätte man damit nicht warfen können, bis von der notorisch an guten Fossilien reichen Fundstelle vollständigere Aufsammlungen vorlagen, besonders wo es sich um ein Land handelt, dessen Erreichung durchaus keine grossen Schwierigkeiten bietet? Wenn gewissermassen ein Gutachten von dem Kenner der alpinen Trias eingefordert wurde, so ist dies ganz in Ordnung; aber weswegen musste gleich alles unter neuen Speziesnamen festgelegt werden? So schmiedet sich die Paläontologie ihre eigenen Ketten."

The author has had the opportunity of examining most of the primary types of each of these species of *Arctoceras* plus a number of additional specimens. The conclusion of this study is that the *Posidonomya* beds of Spitsbergen contain only one species of *Arctoceras*, namely *A. blomstrandi* (Lindström). All the remaining species are either immature forms or morphological variants of a variable species group. In addition, it is concluded that the *Arctoceras* fauna of Spitsbergen is more likely mid-Scythian in age (Owenitan division of Spath) than late Scythian (Columbitan or Prohungaritan of Spath) as believed by most previous authors.

SYSTEMATIC PALEONTOLOGY

ARCTOCERAS BLOMSTRANDI (Lindström)

Plate 1, figs. 1-4; Plate 2, figs. 1, 2; Plate 3, figs. 1-5; Plate 4, figs. 1-4; Plate 5, figs. 1-10; Plate 6, figs.1-4;Plate 7, fig. 1.

Ceratites ? blomstrandi Lindström, 1865, Kongl. Sv. Vet. Akad. Handl., vol. 6, no. 6, p. 4, pl. 1, fig. 3.

Ceratites blomstrandi, Öberg, 1877, Kongl. Sv. Vet. Akad. Handl., vol. 14, no. 14, p. 11, pl. 3, figs. 1-4; Wepfer, 1912, Palaeontographica, vol. 59, p. 7.

Ceratites costatus Öberg, 1877, Kongl. Sv. Vet. Akad. Handl., vol. 14, no. 14, pp. 13-14, pl. 4, fig. 3, *non* 4; Mojsisovics, 1886, Mém. Acad. Imp. Sci. Nat. St. Petersb., ser. 7, vol. 33, no. 6, pp. 36-37, pl. 7, fig. 3; Frech, 1905, Lethaea geognostica, vol. 1, Asiatische Trias, pl. 29, fig. 9; Wepfer, 1912, Palaeontographica, vol. 59, p. 7.

Dinarites öbergi Mojsisovics, 1882, Abh. geol. Reichsanst. Wien, vol. 10, p. 12 (for *Ceratites blomstrandi* in Öberg, 1877, pl. 3, fig. 1).

Ceratites öbergi Mojsisovics, 1886, Mém. Acad. Imp. Sci. Nat. St. Petersb., vol. 33, no. 6, pp. 33-34, pl. 7, figs. 5-6; pl. 8, figs. 1, 3; Frech, 1905, Lethaea geognostica, vol. 1, Asiatische Trias, pl. 29, fig. 7; Wepfer, 1912, Palaeontographica, vol. 59, p. 7.

Ceratites lindströmi Mojsisovics, 1886, Mém. Acad. Imp. Sci. Nat. St. Petersb., vol. 33, no. 6, p. 35, pl. 8, fig. 2; Wepfer, 1912, Palaeontographica, vol. 59, p. 7.

Ceratites simplex Mojsisovics, 1886, Mém. Acad. Imp. Sci. Nat. St. Petersb., vol. 33, no. 6, pp. 30-31, pl. 6, figs. 2-4; Wepfer, 1912, Palaeontographica, vol. 59, p. 7.

Ceratites polaris Mojsisovics, 1886, Mém. Acad. Imp. Sci. Nat. St. Petersb., vol. 33, no. 6, pp. 31-32, pl. 7, figs. 1-2; Frech, 1905. Lethaea geognostica, Bd. 1, Asiatische Trias, pl. 29, fig. 8; Wepfer, 1912, Palaeontographica, vol. 59, p. 7.

Ceratites ind. Mojsisovics, 1886, Mém. Acad. Imp. Sci. Nat. St. Petersb., vol. 33, no. 6, p. 32, pl. 6, fig. 7.

Ceratites nov. f. indet., Mojsisovics, 1886, Mém. Acad. Imp. Sci. Nat. St. Petersb., vol. 33, no. 6, p. 37, pl. 7, fig. 4; Öberg, 1877, Kongl. Sv. Vet. Akad. Handl., vol. 14, no. 14, p. 14, pl. 4, fig. 1c (only).

Ceratites whitei Mojsisovics, 1886, Mém. Acad. Imp. Sci. Nat. St. Petersb., vol. 33, no. 6, pp. 32-33, pl. 6, figs. 5-6; Wepfer, 1912, Palaeontographica, vol. 59, p. 7.

Arctoceras blomstrandi, Diener, 1915, Fossilium Catalogus, Part 8, p. 52; Spath, 1921, Geol. Mag., vol. 68, p. 299; Frebold, 1930, Skr. Svalb. og Ishavet, No. 28, pp. 19-20; Spath, 1934, British Museum Catalogue Fossil Cephalopoda, Part 4, pp. 259-260.

Arctoceras costatus, Diener, 1915, Fossilium Catalogus, Part 8, p. 52; Spath, 1921, Geol. Mag., vol. 68, p. 299; Spath, 1934, British Museum. Catalogue Fossil Cephalopoda, Part 4, pp. 262-263.

Arctoceras öbergi, Diener, 1915, Fossilium Catalogus, Part 8, p. 52; Spath, 1921, Geol. Mag., vol. 68; p. 299; Frebold, 1930, Skr. Svalb. og Ishavet, No. 28, p. 19; Spath, 1934, British Museum Catalogue Fossil Cephalopoda, Part 4, pp. 261-262.

Arctoceras lindströmi, Diener, 1915, Fossilium Catalogus, Part 8, p. 52; Spath, 1921, Geol. Mag., vol. 68, p. 299, 302; Spath, 1934, British Museum Catalogue Fossil Cephalopoda, Part 4, pp. 263-264, fig. 88c.

Arctoceras simplex, Diener, 1915, Fossilium Catalogus, Part 8, p. 52; Spath, 1921, Geol. Mag., vol. 68, p. 299; Spath, 1934, British Museum Catalogue Fossil Cephalopoda, Part 4, p. 259.

Arctoceras polare, Diener, 1915, Fossilium Catalogus, Part 8, p. 52; Spath, 1921, Geol. Mag., vol. 68, p. 299; Spath, 1934, British Museum Catalogue Fossil Cephalopoda, Part 4, pp. 257-259, fig. 88a-b.

Arctoceras sp. ind. Mojsisovics. Diener, 1915, Fossilium Catalogus. Part 8, p. 53.

Arctoceras whitei, Diener, 1915, Fossilium Catalogus, Part 8, p. 53; Spath, 1921, Geol. Mag., vol. 68, p. 297; Frebold, 1930, Skr. Svalb. og Ishavet, No. 28, pp. 18-19, pl. 5, figs. 1-3; Spath, 1934, British Museum Catalogue Fossil Cephalopoda, Part 4, pp. 260-261, fig. 89.

The illustrations of the primary types of the various species of *Arctoceras* described by Lindström, Oberg, and Mojsisovics are for the most part highly idealized drawings. These illustrations plus the accompanying descriptions (mostly brief diagnoses) by these authors are all that most students of Triassic ammonites have had available to appraise the Spitsbergen fauna. Because the original illustrations are so misleading, each of the primary types is illustrated here by unretouched photographs. In addition each of these specimens is described in terms of its preservation etc., before the group as a whole is discussed.

Ceratites blomstrandi Lindström (1865, p. 4, pl. 1, fig. 3; Mojsisovics, 1886, pp. 29-30, pl. 6, fig. 8; Pl. 1, figs. 1-2 of this report).

A poorly preserved specimen of 74.0 mm. in diameter consisting of the phragmocone and slightly less than half a whorl of body chamber. Only one side of the specimen is preserved, showing some sutures and areas where the shell is preserved. The opposite side of the conch preserves only the phragmocone to a diameter of approximately 49.0 mm. and this portion is preserved in a coarse crystalline calcite which obliterates all details. The adoral quarter whorl of the phragmocone and all of the body chamber on this side of the conch is missing. Thus on the body chamber only portions of the venter are visible. The complete ventral region is only preserved on the phragmocone.

Lindström's original illustration of this specimen is so crude and general that it would be extremely difficult, if not impossible, to identify this specimen with the drawing. A portion of the living chamber is missing leaving a wide gap; the remaining piece of the body chamber is crushed and has been glued into place. Lindström's drawing does not include this adoral portion of the living chamber. The illustrations in Mojsisovics (1886, pl. 6, figs. 8a-c) are superior but highly idealized. For instance, the view of the best preserved side (Fig. 8a) shows the body chamber completely reconstructed with no indication of the crushing or the piece that is missing. The view of the opposite side of the conch is a more faithful reproduction of what the specimen actually shows except that the missing segment of the body chamber is not indicated. The front view (Fig. 8c) is reasonably accurate for the portion covering the phragmocone but the cross-section of the living chamber is entirely reconstructed.

The inner whorls of the specimen, encompassing most of the phragmocone, are compressed, discoidal, with briefly arched lateral areas and a well rounded venter. At a diameter of 49 mm. the umbilicus measures 5.5 mm. in diameter. The umbilical shoulder is sharply rounded and, as far as can be told, the umbilical walls are nearly vertical. There is a trace of the umbilical seam for a half whorl beyond the phragmocone and this shows that the conch is gradually becoming more evolute and the umbilical diameter increasing. However, the umbilical shoulder is not preserved beyond a conch diameter of 49 mm. Ornamentation consists of weak radial to slightly sinuous growth lines plus weak strigations which are visible in the region of the venter. The suture of this specimen is reproduced here on Figure 2B.

This specimen came from the *Posidonomya* beds at Midterhuk, Spitsbergen. Mojsisovics (1886, p. 30) states that he had three specimens for study from Midterhuk, the locality of the type specimen, and from Isfjord-Kolonie, Spitsbergen.

Repository. Holotype, NRPAS[1] 247.

Ceratites polaris Mojsisovics (1886, pp. 31-32, pl. 7, figs. 1-2; Pl. 4, figs. 1, 2 of this report).

Hyatt (1900, p. 559) introduced the generic name *Arctoceras* for the group of *Ceratites polaris* Mojsisovics (1886). Later, Diener (1915, p. 52) designated the specimen figured by Mojsisovics (1886, pl. 7, figs. 1a, b) as the holotype. This particular specimen had previously been described and illustrated as *Ceratites blomstrandi* Lindström by Oberg (1877, p. 11, pl. 3, fig. 3).

The holotype is a specimen of approximately 51 mm. in diameter with a quarter whorl of body chamber. Only one side of the conch is preserved, the other side is completely missing and the venter preserved only in two small areas. The body chamber is likewise slightly crushed. Of the two illustrations that have

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[1] Naturh. Riksmus. Paleozool. Avd. Stockholm.

previously been published of this species, that in Öberg (1877, pl. 3, fig. 3) is actually the best even though slightly idealized. It shows the matrix attached to a part of the specimen and general shape and involution of the conch. It does not, however, give a correct impression of the crushed nature of the body chamber or of the suture. The illustration in Mojsisovics (1886, pl. 7, figs. 1a-b) is a completely idealized drawing having little reality with the type specimen.

The conch is discoidal, compressed, with broad, slightly convex lateral areas, rounded ventral shoulders and somewhat narrowly rounded venter. The umbilical shoulders are sharply rounded and the umbilical wall nearly vertical. At a diameter of 44.5 mm. the whorl height is 23.6 mm. and the umbilical diameter 5.0 mm. The lateral areas bear sigmoidal striae of growth. The suture (Fig. 2A) consists of a large first lateral lobe with four denticulations and a smaller, narrow, second lateral lobe with only two denticulations.

The paratype (Mojsisovics, 1886, pl. 7, fig. 2; Pl. 4, fig. 2, of this report) is another specimen whose preservation leaves much to be desired. It consists of slightly more than half the conch — mostly phragmocone — and only one side of the specimen is preserved. Much of the specimen is covered by minute crystals of pyrite. The umbilical region is covered by matrix. The flanks are broad and nearly flattened, the ventral shoulders rounded and the venter arched. The suture is like that of the holotype and is reproduced here on Figure 3C.

Mojsisovics had four specimens for study from the *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen.

Repository. Holotype NRPAS 270, paratype NRPAS 271.

Ceratites simplex Mojsisovics (1886, pp. 30-31, pl. 6, figs. 2-4; Pl. 5, figs. 1-8, of this report).

The three specimens illustrated by Mojsisovics (one only by its suture) plus the specimen assigned by Öberg (1877, p. 11, pl. 3, figs. 4a-c) to *Ceratites blomstrandi*, but included in *C. simplex* by Mojsisovics are available. They are all small, involute, discoidal forms of fair preservation. The illustrations of these specimens by Mojsisovics (1886) and Öberg (1877) are reasonably correct. The measurements of these four specimens are as follows:

	D	W (in mm.)	H	U
Mojsisovics (1886, pl. 6, figs. 3a-b)				
NRPAS 273b	26.3	7.5	13.9	4.5

Öberg (1877, pl. 3, figs. 4a-c)				
NRPAS 278 (lectotype)	25.0	6.5	12.6	4.2
Mojsisovics (1886, pl. 6, fig. 4)				
NRPAS 273c	18.8	5.2	9.8	3.3
Mojsisovics (1886, pl. 6, figs. 2a-b)				
NRPAS 273a	16.3	4.2	9.0	2.3

The lateral flanks are broad and only slightly convex, being bounded by a well rounded ventral shoulder which grades onto a narrowly rounded venter; on the other extreme, the umbilical shoulders are sharply rounded and the umbilical wall nearly vertical. The venter is distinctly more flattened on specimen NRPAS 273a (Mojsisovics, 1886, pl. 6, figs. 2a-b) than on the other specimens producing a more distinct ventral shoulder somewhat resembling the umbilical shoulder.

The lateral areas have weak sinuous growth lines that are periodically accentuated in the dorsal half of the whorl sides. This feature is especially marked on the two larger specimens but barely visible on the two smaller specimens.

Mojsisovics (1886, p. 31) states he had nine specimens for study from the *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen.

Repository. NRPAS 273a, b, c; 278 (lectotype).

Ceratites whitei Mojsisovics (1886, pp. 32-33, pl. 6, figs. 5-6; Pl. 3, figs. 3-4, Pl. 6, fig. 2, of this report).

The holotype and paratype of this species are available for study. The illustrations of these specimens in Mojsisovics' monograph (1886, pl. 6, figs. 5-6) are highly idealized drawings that give no idea of the actual poor preservation of the specimens.

The holotype consists of approximately two-thirds of a volution with the whole umbilical region missing (Pl. 3, figs. 3, 4). The ventral region and half of one flank of the adoral half of the specimen is also not preserved. The cross-section of the whorls is slightly inflated with convex lateral areas, rounded ventral shoulders and sharply rounded umbilical shoulders, and nearly vertical umbilical walls; the whorl section at the most adoral part of the specimen measures 15.4 mm. in width and 24.3 mm. in height. The lateral areas bear low, narrow radial folds that project slightly forward near the ventral shoulders.

The paratype is a small specimen of 36.7 mm. in diameter in which only one side of the conch is preserved and the umbilical region is filled with matrix. The lateral area of the adoral half whorl is crushed. Surface markings are not apparent on the conch, most likely due to the poor preservation of the specimen.

Mojsisovics' two specimens came from the *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen.

Repository. Holotype NRPAS 280, paratype NRPAS 281.

Ceratites öbergi (Mojsisovics) (1882, p. 12; 1886, pp. 33-34, pl. 7, figs. 5-6; pl. 8, figs. 1, 3; pl. 2, figs. 1-2, pl. 3, fig. 5, pl. 4, fig. 3; Pl. 5, fig. 10, of this report).

The four specimens of this species described and figured by Mojsisovics (1886) are available for study. The holotype was designated by Mojsisovics (1882, p. 12) as the large specimen described and illustrated by Öberg (1877, pl. 3, figs. 1a-b; and pl. 8, figs. 3a-b in Mojsisovics, 1886) and thus cannot be the specimen illustrated by Oberg (1877 on pl. 3, figs. 2a-b and in Mojsisovics, 1886, on pl. 7, figs. 3a-b) as indicated by Spath (1934, p. 261).

The illustrations of the holotype in both Öberg (1877) and in Mojsisovics (1886) are fair representations of the specimen, that in Oberg's paper being the better. Neither of these authors shows any portion of the whorl broken off and it may be that a piece of the outer volution was broken off and lost since these authors studied the specimen.

The holotype consists of a fairly well preserved specimen of roughly 116 mm. in diameter of which only the venter and one side of the conch is preserved. The shell is present on most of the specimen except for a small part of the phragmocone. The whorl section has flattened sides, a broadly arched venter, well rounded ventral shoulder, and sharply rounded umbilical shoulder. The conch is evolute, the umbilicus measuring 29 mm. in diameter at the most adoral part of the conch. The umbilical walls are flattened and nearly vertical. The shell bears prominent, slightly sinuous folds or ribs that begin at the umbilical shoulder at a node or tubercle and end on the ventral shoulders. Parallel to the folds are fine growth lines. In addition to these features of ornament the shell on the venter and on the ventral half of the whorl sides bears fine strigations. The suture is reproduced on Figure 2C.

One of the paratypes (Pl. 4, fig. 3) is another of the specimens which Oberg (1877, pp. 11-13, pl. 3, figs. 2a-b) originally assigned to *Ceratites blomstrandi* Lindström. This is a fairly well preserved specimen in which only one side of the conch and the venter are preserved. The specimen measures 71.7 mm. in diameter, approximately 20 mm. for the width of the last whorl.

32.9 mm. for the height of the last whorl and the diameter of the umbilicus is 15.0 mm. The whorl section has the same general shape and features as the holotype. The whorls bear fine sinuous growth lines that are slightly enlarged on the umbilical shoulders forming incipient nodes. On the adoral first centimeter of the umbilical shoulder three prominent tubercles are present, each progressively larger than the preceding one. Slightly sinuous folds or ribs are widely spaced on the inner whorls, then for a half whorl appear to be absent, and finally reappear on the last quarter whorl of the specimen. The suture is reproduced here on Figure 3D.

The third specimen figured by Mojsisovics (1886, pl. 8, fig. 1) is a poorly preserved specimen of roughly half a whorl and really showing well only the umbilical region. Mojsisovics' illustration is highly idealized. The specimen displays the umbilical tubercles and the fine growth lines very well (Pl. 3, fig. 5).

The fourth specimen is a small form of approximately 33 mm. in diameter, embedded in matrix with only one side of the conch exposed. The umbilical shoulder is acutely rounded but no tubercles are present. The whorl sides have very weak, fine, slightly sinuous ribs.

Mojsisovics (1886, p. 34) had for study ten specimens which he assigned to this species which came from the *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen.

Repository. Holotype NRPAS 289, paratypes NRPAS 286, 288, 284.

Ceratites lindströmi Mojsisovics (1886, p. 35, pl. 8, fig. 2; Pl. 7, fig. 1 of this report).

Mojsisovics based this species on a single large specimen of fair preservation in which only one side of the conch is preserved to about the mid-line of the venter. The specimen measures 110 mm. in diameter, 48.6 mm. for the height of the last whorl, and the umbilicus is 26 mm. in diameter. The shell is preserved only in a few small patches. The principal features of the conch are the rather closely spaced slightly sinuous ribs on the whorl sides. On the cast no umbilical tubercles are present but a small piece of shell is preserved on a portion of the umbilical shoulder and there the ribs are slightly enlarged to form a weak elongate tubercle. The inner whorls are very badly preserved but as far as can be told they appear to be smooth, lacking any type of ribs or folds. This, however, may be due to the preservation. The suture is reproduced here on Figure 3B.

Mojsisovics' holotype, and only specimen, came from the *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen.

Repository. NRPAS 266.

Ceratites costatus Öberg (1877, pp. 13-14, fig. 3; Mojsisovics, 1886, pp. 36-37, pl. 7, figs. 3; Pl. 4, fig. 4, of this report).

The holotype and only specimen of this species is a cast, with no shell preserved, of only fair preservation. The specimen measures 77 mm. in diameter, 31.3 mm. for the height of the last whorl, and the umbilicus approximately 22 mm. in diameter. The most conspicuous features of this specimen are the rather prominent, slightly sinuous ribs. On all but the most adoral quarter whorl the ribs are most prominent on the dorsal half of the whorl side but, at least on the cast, do not form a tubercle at the umbilical shoulder. These ribs likewise disappear at the ventral shoulders. On the adoral quarter whorl the ribs are less prominent near the umbilical shoulder and gradually increase in size towards the venter. These ribs completely cross the venter where they are slightly projected forward. The region of the venter just adoral to each of these ribs is broadly constricted. The suture is reproduced here on Figure 3A.

The holotype is from the *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen.

Repository. NRPAS 251.

Ceratites ind. Mojsisovics (1886. p. 32. pl. 6, fig. 7; Pl. 3, fig. 2, of this report).

This small specimen of mediocre preservation was left undetermined by Mojsisovics because the suture is not exposed. The specimen measures approximately 42 mm. in diameter and only one side of the specimen is preserved. The adoral quarter whorl is crushed and the umbilicus occupied mostly by matrix. The lateral areas are broadly arched and the venter narrowly rounded. The umbilical shoulders are sharply rounded and it appears that the umbilical walls are nearly vertical. Sinuous striae of growth are the only markings on the lateral areas.

The figured specimen came from the *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen.

Repository. NRPAS 294.

Ceratites nov. f. indet. Mojsisovics (1886, p. 37, pl. 7, fig. 4; Öberg, 1877, p. 14, pl. 4, fig. 1c; Pl. 6, fig. 1 of this report).

This specimen is so poorly preserved one wonders why it was described at all by Mojsisovics and Öberg. No part of the shell is preserved and the internal cast is imperfect. All of the internal volutions are missing and a half of the outer whorl of phragmocone. Mojsisovics' (1886, pl. 7, fig. 4) illustration is highly idealized.

The most significant feature of this specimen is the rounded umbilical shoulder, and in this feature, plus faint ribs on the living chamber, it shows some similarity to *A. costatum.* The umbilical shoulder is preserved, however, only on the living chamber and in the absence of any shell, care is needed in the interpretation of this feature.

The specimen came from the *Posidonomya* beds, Isfjord-Kolonie, Spitsbergen.

Repository. NRPAS 293.

Remarks.

The primary types of all the various species of *Arctoceras* represent different growth stages of a single species which shows marked variability in its ontogeny. *Arctoceras simplex* (Mojsisovics) was established for the smallest specimens. In addition to the three specimens described and illustrated by Mojsisovics (1886, pp. 30-31, pl. 6, figs. 2-4), he also included in this species a similar small involute form which Öberg (1877, p. 11, pl. 3, fig. 4) had identified as the inner whorls of *Ceratites blomstrandi.* All four of these specimens are involute, compressed forms with broadly convex flanks. The smallest specimen (Pl. 5, figs. 5, 6) has just the faintest trace of radial ornamentation and the ventral shoulders are abruptly rounded and the venter only slightly arched. The two larger specimens of *Ceratites simplex* (Pl. 5, figs. 1, 2, 7, 8) have low, but clearly marked, slightly sinuous ribs that begin at the umbilical shoulder and disappear as they approach the venter. The venter is also more highly arched. This basic conch plan is maintained at a diameter of 31 mm. as illustrated on the specimen of Plate 5, figure 9: it also characterizes the following specimens: the paratype of *Ceratites whitei* (Pl. 6, fig. 2) — diameter 37 mm. — which has a slightly larger umbilicus; the specimen Mojsisovics listed as *Ceratites* ind. (Pl. 3, fig. 2); the inner whorls of the holotype of *Ceratites blomstrandi* (Pl. 1, fig. 2); the plesiotype of Plate 3, figure 1; and the holotype of *Ceratites polaris* (Pl. 4. fig. 1). At its diameter, the whorls of the holotype of *Ceratites whitei* are a little more inflated and the ribs more conspicuous. Above a diameter of approximately 50 mm., there is an even greater degree of variation in conch shape and ornamentation. On the one hand, there are forms of 69 mm. in diameter (Pl. 6, fig. 4) which maintain the pattern of the youthful forms except that the umbilicus becomes broader and deeper. Ornamentation consists of narrow, closely spaced ribs or bunched growth lines. The umbilical slope is not quite vertical and the umbilical shoulder sharply rounded but lacking nodes. Somewhat similar conch pattern is displayed by the paratype of *Ceratites blomstrandi* (Pl. 1, figs. 3, 4) except that in this specimen the umbilical shoulder is more sharply rounded, the sinuous lateral ribs more prominent and the ribs are slightly enlarged at the umbilical shoulder. The paratype of *Ceratites öbergi* (Pl. 4, fig. 3) is also quite similar but on this specimen the umbilical wall is vertical and nodes are apparent on the most adoral part of the umbilical shoulder. The nodes on the other paratype of *Ceratites öbergi* (Pl. 3, fig. 5) appear earlier and are more conspicuous. These latter forms grade into the type of conch of the large holotype of *Ceratites öbergi* (Pl. 2, figs. 1, 2).

Ceratites costatus (Pl. 4, fig. 4) is quite distinctive in its larger umbilicus and coarser lateral ribs which cross the venter on the most adoral quarter whorl. None of the shell is preserved on this specimen. The large, poorly preserved specimen which represents the holotype of *Ceratites lindströmi* (Pl. 7, fig. 1) also has prominent coarse lateral ribs such as those in *Ceratites öbergi*. The venter of the adoral half whorl of this specimen is not preserved but there is a suggestion that the ribs do cross the venter. The portion of the inner whorls that is visible is without ribs.

Discrimination of the various species of *Arctoceras* on the basis of conch shape, degree of involution, etc. was attempted by earlier authors. On Figure 1, are plotted the measurements of the height of last whorl and umbilical diameter of 202 specimens of *Arctoceras* from Spitsbergen, identified by L. F. Spath, in the British Museum (Natural History). This includes 141 specimens of *A. blomstrandi*, 41 specimens of *A. whitei*, 11 specimens of *A. polare*, 8 specimens of *A. costatum*, and 1 specimen of *A. öbergi*. In addition, the numbered points are for thirteen primary types of the various species of *Arctoceras*. The range of variation within each of the "so-called" species is roughly the same and these ranges overlap one another. Nor are any significant differences apparent between the various growth stages. It is not possible on the basis of these two measurements to differentiate the seven species of *Arctoceras* previously recognized; the data supports the conclusion that this is a single species complex.

Additional data on the degree and kind of ornamentation on the 202 specimens in the British Museum (Natural History) are not available. However, from a study of the primary types, the differences in ornamentation are merely a matter of degree and merely a matter of the stage of ontogenetical development of the particular specimen. The ribbing ranges from fine to coarse, narrow to broad, and appears at varying times in the development of the conch. Spath's (1934) description of some of the Spitsbergen arctoceratids repeatedly emphasizes the gradational nature of conch form and ornamentation between all the various species.

The suture was one of the primary features Mojsisovics used to differentiate his various species. The suture of each of the seven primary types is illustrated on Figures 2 and 3. The number of denticulations on the lobes, the shape of the lobes, etc. are hardly proper criteria for separation of species in forms like this that occur in the same place and geological horizon Spath (1934, p. 262) records a specimen of *A. öbergi* in which the number of denticulations in the lobes varies on opposite sides of the same individual. It was criteria such as this — the number of denticulations of the lobes — that Mojsisovics used to distinguish some of his species. The differences in the sutures as shown in Figures 2 and 3 are due to differences in the growth stage at which the suture was taken or are merely the normal variations one should expect in a variable population.

The most closely related species to these Spitsbergen arctoceratids are forms from the Arctic islands of Canada which Tozer (personal communication) is placing in *Arctoceras öbergi.* In addition, *Meekoceras tuberculatum* Smith (1932) is remarkably similar. Smith based his species on two highly deformed specimens from the *Meekoceras* beds, Union Wash, Inyo Range, California (Pl. 8, figs. 1, 2). The writer has in press a study of a large, excellently preserved *Meekoceras* fauna from Elko County, northeastern Nevada. This fauna has yielded a number of well preserved specimens which are conspecific with *Meekoceras tuberculatum.* Study of these specimens has given a better appreciation of the amount and kind of variation to be found in species of this conch morphology.

In these Nevada specimens the conch is evolute with slightly convex, broad lateral areas and a broadly rounded venter (Pls. 8, 9). The ventral shoulders are rounded, grading imperceptibly onto the venter and the flanks of the whorl section. The umbilical shoulders are sharply rounded and conspicuous, the umbilical walls flat and nearly vertical. The most characteristic features of this species are the nodes on the umbilical shoulders. The nodes are spaced roughly 10 mm. apart along the umbilical shoulder and appear to vary considerably in size. In addition to these nodes, the conch bears radial folds on the flanks which likewise show great variation in strength and numbers. Some forms have prominent radial ribs, widely spaced, others have less prominent but closely spaced ribs. Other forms appear to be almost smooth but with weak, low, broad folds. On the better preserved specimens, weak strigations are visible. Juvenile specimens up to a diameter of at least 40 mm. have no ornamentation, lacking the radial folds and the umbilical tubercles.

The height of the whorl section and the diameter of the umbilicus for thirteen specimens are plotted on Figure 4.

The suture has a broad denticulated ventral lobe, a relatively narrow, long, first lateral lobe, a narrow, short, second lateral lobe and a short differentiated auxiliary series; the first lateral saddle is broad and rounded, the second lateral saddle is equally rounded but not so broad (Fig. 5A). The suture of juvenile forms (25 mm. in diameter) in contrast to the more mature suture has relatively narrow phylloid saddles (Fig. 5C) but the saddles change rapidly into broad, rounded forms. The suture of Smith's holotype and that of a paratype are reproduced here on Figure 5D, E; that of the holotype is nearly identical to the Crittenden Spring specimen except for slight differences in the pattern of denticulations of the second lateral lobe and in the auxiliary series. The suture of the paratype as drawn by Smith has denticulations extending half way up the sides of the lobes. The fact that the Inyo Range specimens are so deformed opens the question as to whether this particular pattern is not a reflection of distortion rather than the true pattern.

The suture of *Arctoceras tuberculatum* is of the same basic plan as that of *Arctoceras blomstrandi.* Separation of these forms into distinct genera, as advocated by Spath (1934) on the basis of differences in the suture, especially the saddles, is untenable. The immature suture of *A. tuberculatum* does have saddles quite distinct from sutures of specimens of comparable size of *A. blomstrandi.* It is on the basis of the suture up to a diameter of roughly 30 mm. and the slightly greater inflation of the conch at this size that *A. tuberculatum* is kept distinct from *A. blomstrandi.* I do not believe that these two species could be differentiated without data on the inner whorls.

The Age of the *Arctoceras* Fauna

With this analysis of the Spitsbergen arctoceratids it seems appropriate to comment briefly on the stratigraphic position of the *Arctoceras* fauna and associated Lower Triassic faunas of Spitsbergen. For much of the recent stratigraphical and paleontological work on the Triassic of this area we look to the fine publications of Frebold (1929a, 1930, 1931, 1939); Spath (1921, 1934) has also commented extensively on the ammonoids of Spitsbergen and their stratigraphic relationships.

The early Scythian of Spitsbergen is represented mainly by pelecypods (*Myalina, Anodontophora, Gervilleia, Eumorphotis, Aviculopecten*), a few brachiopods (*Terebratula, Retzia, Orbiculoidea*), a bellerophon, and indeterminate ammonoids (Frebold, 1939). The lowest horizon that contains an identifiable ammonoid fauna is the *Posidonomya* Beds (or Fish-horizon, see Frebold, 1930, p. 31) and most of the Lower Triassic ammonoids from Spitsbergen have come from this stratigraphic unit. Frebold (1930) came to the conclusion that there were two distinct ammonoid faunas in the *Posidonomya* Beds, a lower and an upper. The lower ammonoid fauna contains the following species (Frebold, 1930; Spath, 1921, 1934):

Arctoprionites nodosus (Frebold)
Arctoprionites tyrelli Spath
Arctoprionites n. sp.
Xenoceltites subevolutus Spath
Xenoceltites gregoryi Spath
Xenoceltites spitsbergensis Spath
Hemiprionites garwoodi Spath
Gurleyites freboldi Spath
Wasatchites tridentinus Spath

The ammonoid fauna of the upper part of the *Posidonomya* Beds is characterized by the following species:

Arctoceras blomstrandi (Lindström)
Prosphingites spathi Frebold
Tellerites oxynotum Frebold
Tellerites furcatus (Oberg)
"*Meekoceras*"? cf. *keyserlingi* Mojsisovics
Pseudosageceras grippi Frebold

Frebold (1930) concluded that the lower fauna was equivalent to that of the Ceratite sandstone of the Salt Range, Pakistan (*Flemingites flemingianus* zone) and in part to the *Hedenstroemia* beds of the Himalayas. The upper fauna Frebold considered as equivalent in part to the fauna of the Olenek Beds, Siberia, and to the *Columbites* fauna of southeastern Idaho. Spath (1934) listed many of the species in the lower fauna as upper Owenitan (*Anasibirites* zone) in age but the various species of *Xenoceltites* and other forms he placed in his Columbitan division with a question mark. The upper fauna was listed as Columbitan in age with question, presumably suggesting the possibility of it being younger (Spath, 1934, pp. 257, 258).

The genera of the lower fauna are all forms typical of *Anasibirites* faunas throughout the world, even though the name genus *Anasibirites* does not appear to be present. The *Anasibirites* fauna has been recognized in Utah (Mathews, 1929), Idaho (Kummel. 1954), British Columbia (McLearn. 1945), Queen Elizabeth Islands (Tozer, 1958), Shikoku, Japan (Yehara, 1928), Hupeh, China (Tien, 1933), Kiangsu, China (Hsu, 1936), Timor (Welter, 1922), Salt Range, Pakistan (Waagen, 1895), and at Byans in the Himalayas (Krafft and Diener, 1909). Spath (1921) tentatively assigned some of his Spitsbergen specimens to *Anasibirites* but later (Spath, 1934, p. 346) he commented as follows on these specimens: "The Spitsbergen forms are now included in *Arctoprionites*, since they are connected by transitions with the other forms of that new genus, but they might perhaps have been left in *Anasibirites*, like the equally discoidal and "*Meekoceras*"-like *A. multiformis*, form VIII (Welter, 1922, pl. clxxi, figs. 8-10), or some of v. Krafft's incompletely known Himalayan species."

Arctoprionites — type species, *Goniodiscus nodosus* Frebold (1930, pp. 8-11, pl. 1, figs. 6-7; pl. 2, fig. 2) — was established for a small group of species from Spitsbergen. It is a prionitid with a discoidal conch, a tabulate venter and bearing costations or tuberculations on the whorl sides. No other species, than those from Spitsbergen, were assigned to this genus by Spath. The writer has a single, well preserved, though incomplete specimen from the *Meekoceras* zone near Montello, Nevada, which will be described in a paper now in press. The form described by McLearn (1945) as "*Prionites*" *hollandi* most likely belongs to this genus, even though, as remarked by that author, the tubercles are closer to the umbilical shoulder and the venter is not as tabulate as in *Arctoprionites.* The specimen described by Diener (1913) as *Flemingites* (?) sp. ind. aff. *muthensis* Krafft, from Kashmir, is also most probably a species of *Arctoprionites.*

Hemiprionites has a very widespread distribution. Species of this genus are known from the Upper Ceratite Limestone of the Salt Range (Waagen, 1895), the *Anasibirites* beds of Timor (Welter, 1922), the *Anasibirites* fauna on Shikoku, Japan (Yehara, 1928), the *Anasibirites* zone near Fort Douglas, Utah (Mathews, 1929), the *Anasibirites* zone near Georgetown, southeastern Idaho (Kummel, 1954), and from the *Anasibirites* fauna in the Toad formation, along the Liard River, British Columbia (McLearn, 1945).

Gurleyites is known from the *Anasibirites* fauna of Fort Douglas, Utah (Mathews, 1929), near Georgetown, southeastern Idaho (Kummel, 1954), and from the lower fauna of the *Posidonomya* Beds of Spitsbergen (Frebold, 1930; Spath, 1934).

Wasatchites is likewise known from typical *Anasibirites* faunas in Utah, Idaho, British Columbia, Queen Elizabeth Islands, Timor, and in Spitsbergen.

Of the original fauna from Spitsbergen studied by Spath (1921) the largest single taxon consisted of specimens which were regarded as an unnamed group for which he later (Spath, 1930, pp. 12, 90) proposed the generic name *Xenoceltites* — type species, *Xenoceltites subevolutus* Spath = *Xenodiscus* cf. *comptoni* (non Diener), Frebold, 1930, p. 14, pl. 3, fig. 1 (lectotype), 2, 3. Spath also recognized congeneric species in the *Anasibirites* fauna of Fort Douglas, Utah, and in the fauna from the Ussuri Bay region described by Diener (1895). Kiparisova (1945) reports unnamed species of *Xenoceltites* from the south Ussuri region (near Vladivostok) in approximately mid-Scythian horizons. McLearn (1945) has also described two species of *Xenoceltites* from the *Anasibirites* zone of British Columbia.

Spath (1934) came to the conclusion that all of the various *Anasibirites* faunas were not contemporaneous and that the Spitsbergen fauna, for example, was probably slightly younger than that from Utah. For my own part, there does not seem to be any real justification for this conclusion. At a generic level all of these *Anasibirites* faunas are remarkably similar. *Hemiprionites, Gurleyites,* and *Wasatchites* are known only from this zone. *Arctoprionites* and *Anasibirites* appear to range from the *Meekoceras* zone to the *Anasibirites* zone. *Xenoceltites* appears to be mainly confined to this zone but it is likely that it ranges lower and higher in the Scythian.

The age of the *Arctoceras* fauna from Spitsbergen is much more difficult to assess. Frebold (1930) considered this fauna to be approximately equivalent to the Olenek fauna of Siberia and to the *Columbites* fauna of southeastern Idaho. Spath (1934) classified the *Arctoceras* fauna as belonging to his Columbitan division with question, suggesting that it was younger than the *Columbites* fauna of Idaho. The fauna comprises only four species in addition to the name-giving *Arctoceras blomstrandi*. These additional species are, however, not as helpful in the dating problem as one could wish. *Tellerites* is as yet incompletely known, that is, few specimens have been found and all of these are small specimens which possibly could represent immature forms. The occluded, compressed conch with the narrow, channeled venter is quite unlike any other Lower Triassic ammonoid. *Tellerites oxynotum* Frebold (1930, pp. 22-23, pl. 4, fig. 4) is also most probably not congeneric with *T. furcatum* (Öberg). Likewise, the form assigned by Frebold (1929b) to *Pseudosageceras grippi* could possibly be a *Tellerites*. The form assigned by Frebold (1930, p. 18) to *Meekoceras* cf. *keyserlingi* Mojsisovics lacks the suture. Whereas the Spitsbergen specimen does resemble the Olenek specimen, there is such homeomorphy among middle and upper Scythian ammonoids of this morphology that without the suture and an abundance of material this identification can only be looked upon as tentative. This leaves only *Prosphingites spathi* and *Arctoceras blomstrandi* upon which one can establish some basis for an age assignment for the fauna.

The genotype of *Prosphingites* is *P. czekanowskii* Mojsisovics (1886, p. 64, pl. 15, fig. 10-12) from the region of the mouth of the Olenek River, Siberia. The inner whorls are globular but the outer whorls more compressed and the venter narrowly opened. The Spitsbergen species are unquestionably prosphingitids but differ from the type species in their more rounded and depressed whorl section at maturity. They are clearly a different species. At the time Spath published his catalogue (1934), he recognized *Prosphingites austini* (Hyatt and Smith, 1905, pp. 72, 73) from the zone of *Meekoceras gracilitatus* in California as most likely being the oldest known species. The genus is also present in the faunas of the *Prohungarites* zone from Albania (Arthaber, 1911), Chios (Renz and Renz, 1948) and Ussuri Bay of eastern Siberia (Kiparisova, 1947) but the species in these faunas are very distinct from those of either Spitsbergen or the Olenek River region. This left the range of *Prosphingites* as definitely including the upper part of the Scythian but only questionably extending as low as the zone of *Meekoceras gracilitatus.* The genus, however, is more widespread in the *Meekoceras* zone of Nevada and Idaho than has been suspected. The writer has in press a report on a large *Meekoceras* fauna of excellent preservation from Elko County, Nevada, that contains a large number of specimens assigned to a new species of *Prosphingites.* This clearly established that *Prosphingites* is well represented in the *Meekoceras gracilitatus* zone and extends upwards through the remainder of the Scythian. These Nevada specimens are more like the Spitsbergen *Prosphingites spathi* than the Olenek, *P. czekanowskii.* In previous analysis of the age of the *Arctoceras* fauna, the fact that the generic assignment of the California *Prosphingites austini* was open to question and the definitely identified prosphingitids came from horizons of the *Prohungarites* zone rightly had a strong influence in placing the *Arctoceras* fauna high in the Scythian.

More satisfactory results can be attained by analyzing *Arctoceras blomstrandi.* Spath (1934, p. 254) maintained that *Arctoceras* was quite distinct from *Submeekoceras* on the basis of its broader saddles. Restudy of the type specimens of the various "species" of *Arctoceras* from Spitsbergen fails to substantiate Spath's conclusion. The range of variation in the suture in both the American species of *Submeekoceras* and of the Spitsbergen *Arctoceras* preclude any attempt to differentiate them on the basis of the suture. The resemblance in both suture and conch morphology of the Spitsbergen *Arctoceras* to *Meekoceras tuberculatum* Smith (1932, p. 62, pl. 50, figs. 1-4) is indeed remarkable. Smith unfortunately based his species on a deformed specimen from the *Meekoceras* zone exposed in the Inyo Range, California. The new fauna of the *Meekoceras* zone from Elko County, Nevada, has numerous large examples of this same species and on direct comparison with the types of the Spitsbergen species of *Arctoceras,* the differences apparent are of no more than specific significance. The genus *Submeekoceras* Spath (1934, p. 255) should be suppressed in favor of *Arctoceras* Hyatt (1900, p. 559). Confirmation of this interpretation of *Arctoceras* has been established by Tozer (1958 and personal communication) from his studies of a splendid sequence of faunas in Triassic sections in the Queen Elizabeth Islands (mainly on Ellesmere and Axel Heiberg islands). One of the fifteen distinct faunas recognized by Tozer contains *Meekoceras*, *Arctoceras*, *Euflemingites*, *Pseudosageceras*, etc. What is most significant about this fauna is the presence in the same beds on Ellesmere Island of *Meekoceras gracilitatus* and *Arctoceras oebergi* (Tozer, personal communication). This fauna is overlain by faunas with *Wasatchites* and the latter by *Olenekites*.

From what we know of the *Arctoceras* fauna at the moment, it shows more affinity with the fauna of the *Meekoceras* zone of western North America than with other known Scythian fauna. However, if the Spitsbergen *Arctoceras* fauna occurs above a fauna of the *Anasibirites* zone as stated by Frebold it cannot be contemporaneous with the zone of *Meekoceras gracilitatus*. It appears to the writer, however, that it is more likely that the *Arctoceras* fauna is related to the faunas of the middle Scythian zones, the *Owenitan* of Spath (1934, p. 27) rather than to the higher Scythian zones comprising Spath's Columbitan and Prohungaritan divisions. The strong similarities of both the *Arctoceras* and *Anasibirites* faunas of Spitsbergen to the *Meekoceras* and *Anasibirites* faunas of western United States (and northern Canada) forces one to question whether the faunal sequence of the *Posidonomya* beds of Spitsbergen has been interpreted correctly. At least additional field observations are needed to clarify this issue. If Frebold's conclusion on the stratigraphic relations of these two faunas is correct, then the *Arctoceras* fauna most likely represents a new zone of Owenitan age, lying above the *Anasibirites* zone and below that of *Tirolites*. The remainder of this discussion is a review of the known upper Scythian ammonoid faunas of the world to demonstrate the impossibility of correlating the *Arctoceras* fauna with any zone other than those of Owenitan age.

One of the best areas of exposure of fossiliferous Scythian strata is to be found in southeastern Idaho. In this region the stratigraphy is well known (Kummel, 1954) and all three of the Upper Scythian ammonoid zones are represented. The *Tirolites* fauna is known only from Paris Canyon about 800 feet above the lower limestone member of the Thaynes formation that contains the *Meekoceras* fauna. Smith (1932) identified the following ammonoid species from this zone:

Dalmatites attenuatus Smith
Tirolites harti Smith
Tirolites knighti Smith
Tirolites pealei Smith

The *Columbites* fauna occurs in the middle shale unit of the Thaynes formation and it includes the following species (Smith, 1932; Kummel, 1954):

"*Ophiceras*" *jacksoni* Hyatt and Smith
"*Ophiceras*" *spencei* Hyatt and Smith
"*Meekoceras*" *curticostatum* Smith
"*Meekoceras*" *micromphalus* Smith
"*Meekoceras*" *pilatum* Hyatt and Smith
"*Meekoceras*" *sanctorum* Smith
Hellenites idahoense (Smith)
Tirolites cf. *T. illyricus* Mojsisovics
Pseudosageceras multilobatum Noetling
"*Celtites*" *apostolicus* Smith
"*Celtites*" *planovolvis* Smith
"*Celtites*" *ursensis* Smith
Columbites consanguineus Smith
Columbites ligatus Smith
Columbites minimum Smith
Columbites ornatus Smith
Columbites parisianus Hyatt and Smith

Finally, the *Prohungarites* fauna occurs approximately 1000 feet above the *Columbites* beds. In this fauna the following species have been identified (Kummel, 1954).

Prohungarites n. sp. cf. *P. similis* Spath
Prohungarites n. sp. cf. *P. crasseplicatus* (Welter)
Svalbardiceras sp.
Metahedenstroemia n. sp.
Keyserlingites n. sp. cf. *K. subrobustus* (Mojsisovics)
Isculitoides n. sp.
Epiceltites n. sp. cf. *E. genti* Arthaber
Czekanowskites ? sp.
Stacheites sp.
Olenekites ? sp.

Since this Idaho succession is in general more complete in terms of the faunas present and the stratigraphic data it will be used in this discussion as a standard of reference.

Each of these faunas is quite distinct from the *Arctoceras* fauna of Spitsbergen; in fact, there is really not a single genus in common between these Idaho faunas and the Spitsbergen fauna. The extremely important faunas being studied by Tozer (1958) from the Queen Elizabeth Islands include the *Meekoceras* fauna (containing *Arctoceras*), the *Wasatchites* fauna (= *Anasibirites* zone), and the *Olenekites* fauna (= *Prohungarites* zone). Note that here *Arctoceras* is associated with the *Meekoceras* fauna and that from the data available there is nothing in the two other faunas to show any affinities with the *Arctoceras* fauna of Spitsbergen.

The Siberian coastal region around the lower parts of the Olenek and Lena Rivers has been well known to students of Triassic ammonoids through the monographs of Mojsisovics (1886, 1888). At the same time, the large Scythian fauna described by Mojsisovics from the lower Olenek River region has long been a source of controversy in respect to its age. Recently, Popov (1958) has published a valuable synthesis of the stratigraphy and faunal content of the Lower and Middle Triassic strata in this part of Siberia. The oldest Triassic strata known from this region are tuffaceous sandstones, shales, and tuffs that contain species of *Estheria* and plant remains. These strata are known from only two regions: the first is the Ulahan-Yuryak region in the lower part of the Lena River, and the second is the Pur River, a tributary entering the lower Olenek River from the west. In both regions these early Triassic deposits rest disconformably on Permian sandstones. Above this lower tuffaceous member in the Ulahan-Yuryak region are 60 meters of black shale with coquinoid beds of *Posidonia* sp., *Posidonia miner* Öberg, and *Glyptophiceras* (?) sp. ind. In the Pur-Olenek region the unit overlying the basal tuffaceous strata is composed of shales, sandstones, and marls with limestone concretions. Some of the sandstone beds contain abundant *Myalina* ex. gr. *schamarae* Bittner. The shale and marl beds contain, according to Popov (1958), *Paranorites olenekensis* Kiparisova (*n. nudum*), *P.* aff. *olenekensis* Kiparisova, *Clypeoceras gantmani* Kiparisova (*n. nudum*), *Glyptophiceras* (?) sp. ind., *Ophiceras Lytophiceras*) sp. ind., *Metophiceras* (?) sp., and *Hedenstroemia mojsisovicsi* Diener. Popov concluded that this fauna was mid-Scythian in age, equivalent to the *Hedenstroemia* beds of the Himalayas and the Salt Range. Evaluation of this fauna is difficult, because aside from *Hedenstroemia mojsisovicsi* none of the species have been described or illustrated. However, the presence of large *Hedenstroemia* and *Clypeoceras* certainly suggests a mid-Scythian age. Popov (1958) correlated these units with a horizon in the Okhotsk-Kolyma land that contains (Popov,

1939) *Pseudosageceras multilobatum* Noetling, *Anahedenstroemia tscherskii* Popov, *Paranannites globosus* Popov, *Ophiceras* (*Lytophiceras*) *subleptodiscus* Popov. At a later date Popov (1958) added *Hedenstroemia mojsisovicsi* to this faunal list. Popov correlated his fauna from the Okhotsk-Kolyma land with the *Meekoceras* beds of California and Nevada, the *Hedenstroemia* beds of the Himalayas, and the Upper Ceratite sandstone of the Salt Range, units which I do not believe are strictly contemporaneous. The *Hedenstroemia* beds of the Himalayas and the *Meekoceras* fauna of western United States are more likely contemporaneous but the Salt Range fauna may represent the next older zone.

Overlying the beds with mid-Scythian ammonoids are up to 200 meters of black shales and marls with concretions and green-gray sandstones. These beds contain the classic Olenek fauna described by Mojsisovics (1886, 1888). This fauna includes the following species:

Olenekites spiniplicatus (Mojsisovics)
Olenekites volutus (Mojsisovics)
Olenekites densiplicatus (Mojsisovics)
Olenekites altus (Mojsisovics)
Olenekites intermedius (Mojsisovics)
Olenekites laevis (Mojsisovics)
Olenekites sigmatoidus (Mojsisovics)
Xenoceltites glacialis (Mojsisovics)
Xenoceltites multiplicatus (Mojsisovics)
Xenoceltites hyperboreus (Mojsisovics)
Xenoceltites fissiplicatus (Mojsisovics)
Xenoceltites discretus (Mojsisovics)
Keyserlingites middendorffi (Keyserling)
Keyserlingites schrencki (Mojsisovics)
Keyserlingites subrobustus (Mojsisovics)
Czekanowskites decipiens (Mojsisovics)
Czekanowskites inostranzeffi (Mojsisovics)
Sibirites eichwaldi (Keyserling)
Sibirites pretiosus (Mojsisovics)
Arctoceras euomphalus (Keyserling)
Svalbardiceras schmidti (Mojsisovics)
"*Xenodiscus*" *dentosus* (Mojsisovics)
"*Xenodiscus*" *karpinskii* (Mojsisovics)
"*Meekoceras*" *keyserlingi* (Mojsisovics)
"*Meekoceras*" *rotundatum* (Mojsisovics)

"*Meekoceras*" *sibiricum* (Mojsisovics)
Prosphingites czekanowskii (Mojsisovics)
"*Popanoceras*" indet.

The age of this fauna has long been a source of debate but stratigraphic and paleontological studies in North America over the past decade have helped to clarify this problem immensely. The key to the understanding of the Olenek fauna is the sequence of faunas in southeastern Idaho where the uppermost ammonoid zone contains *Olenekites, Czekanowskites, Keyserlingites,* and *Svalbardiceras.* The first two of these genera are represented by poorly preserved specimens and there was at first some question as to these identifications. The *Prohungarites similis* fauna of southeastern Idaho represents a mixture of the boreal Olenek fauna and the Tethyan Albania-Chios-Timor faunas. A similar fauna, of splendid preservation (including *Olenekites*), is known from the Tobin formation of Nevada (S. W. Muller, personal communication). Likewise Tozer (1958) reports *Olenekites* at the top of the Scythian sequence in the Arctic islands of Canada. There is no question but that Spath (1934) was correct in placing the Olenek fauna high in the Scythian, above the zone of *Columbites parisianus.*

The *Arctoceras* fauna of Spitsbergen has in common with the Olenek fauna: *Prosphingites*, *Arctoceras*, and the doubtful "*Meekoceras*" cf. *keyserlingi. Prosphingites* is a long-ranging genus and the Spitsbergen and Olenek species are quite different. The arctocerid *A. euomphalus* (which Mojsisovics, 1886, originally placed in *Xenodiscus*) represents a morphological type that occurred repeatedly in the Upper Scythian. It would be inadvisable to place any credence on this form for purposes of correlation. As mentioned earlier, the identification of "*Meekoceras*" cf. *keyserlingi* from Spitsbergen is open to question. There does not seem to be any basis whatsoever on which to compare directly the *Arctoceras* fauna of Spitsbergen and the Olenek fauna of Siberia; this is due, in my opinion, to their complete difference in age.

Extensive outcrops of Lower Triassic strata in the south Ussuri coastal region around Vladivostok have attracted the attention of numerous Triassic students ever since Diener (1895) first monographed the ammonites from this region. In addition to ammonites, these strata contain a rich and diverse fauna of pelecypods which have been monographed by Kiparisova (1938). The stratigraphy of these Lower Triassic formations has been summarized by Kiparisova (1945), who recognized four main beds which, from bottom to top, she referred to as (a) the Basal bed, (b) *Meekoceras* beds, (c) *Flemingites* beds, and (d) the *Subcolumbites* beds. Only the two upper units need concern us here. Most of the species listed by Kiparisova in her 1945 paper were *nomina nuda* and were not formally described until 1947.

The *Flemingites* beds consist of thin bedded sandstones containing *Flemingites prynadi* Kiparisova (1947), *Proptychites latifimbriatus* (de Koninck) Kiparisova (1947) plus a large fauna of small pelecypods. This horizon Kiparisova correlated with the Ceratite sandstone of the Salt Range, the *Hedenstroemia* beds of the Himalayas and the *Meekoceras* zone of western North America — again, horizons which are probably not contemporaneous.

It appears that the thickness and aerial extent of the *Flemingites* beds are still unknown for in places it is only one meter thick. On the Russian Island the "*Meekoceras*" beds are overlain by thin-bedded sandstones alternating with clay shales. In the lower part of this sequence occurs *Tropiceltites inopinatus* Kiparisova (*n. nudum*). A limestone band 30-40 meters higher contains *Subcolumbites multiformis* Kiparisova (1947), *Prosphingites glòbosus* Kiparisova (1947), *Megaphyllites immaturus* Kiparisova (*n. nudum*), *Paranannites suboviformis* Kiparisova (*n. nudum*), *Paranannites gracilis* Kiparisova (1947), *Pseudosageceras simplex* Kiparisova (1947), *Grypoceras ussuriense* Kiparisova (1947), and *Orthoceras subcampanile* Kiparisova (*n. nudum*). This fauna Kiparisova correctly recognized as of uppermost Scythian age and representing the zone of *Prohungarites similis*.

The widespread occurrence of Lower Triassic formations in south China has long been known, but the lack of comprehensive stratigraphical and paleontological reports, especially on the ammonites, has handicapped interpretation of the record. The only monographic treatment of Lower Triassic ammonoids is by Tien (1933), and small but interesting faunas of ammonoids have been described by Hsu (1936, 1937). A monographic study of the Triassic fossils of Yunnan has apparently been prepared by T. H. Yen and T. Y. Hsu but has never been published (*fide* Hsu, 1937; Hsi-chih, 1947).

Among the faunas described by Tien (1933) was a single specimen from a locality in Kweichow, referred to *Palaeophyllites* cf. *steinmanni* Welter. Previously this particular species has been known only from the *Prohungarites similis* zone of Timor. However, Tien's specimen is quite different, and this suggested identification must be left in doubt.

In a comprehensive report on the Lower Triassic Chinglung limestone exposed in the lower Yangtze Valley around Nanking, Chi, Hsu, and Sheng (1936) recorded two distinct ammonoid zones. Specimens from these zones have been described by Hsu (1936). The lower fauna is of early Scythian age but the upper fauna was said to contain *Xenodiscus* sp., *Tirolites* cf. *spinosus* Mojsisovics, *Tirolites* sp. nov. ind., *Anasibirites* sp., and *Celtites* sp. Hsu (1936) interpreted these faunas as representing the *Anasibirites* and *Tirolites* zones; however, from the description and illustrations, the tirolitids and celtitids appear to belong to *Xenoceltites.* If this determination is correct, it appears unlikely that the *Tirolites* zone is represented.

What appears to be potentially the largest and zonally the most complete representation of Lower Triassic ammonoids in south China has been recorded by Chao (1947) from western Kwangsi. Aside from a statement that these faunas contain more than 60 genera, little is known except the illustrations and description of a few new genera (Chao, 1950).

The youngest Scythian ammonoid fauna known from Japan is that described by Yehara (1928) representing the *Anasibirites* zone.

The glamor of the beautifully preserved and diverse Scythian faunas from Timor is slightly tarnished by the lack of any stratigraphic data. As pointed out by Spath (1934, pp. 30, 31), the bulk of Welter's (1922) Scythian ammonoids belong to about the mid part of that stage, but one fauna, that from Block "E" bei Nifoekoko which Welter placed about equivalent to his *Owenites* limestone, Spath placed as at or near the top of the Scythian. The name genus of Spath's Prohungaritan division and the one zone assigned to this division was based on a species from Block "E" bei Nifoekoko. It is unfortunate that the name bearing specimens for this division and zone came from a unit on which no stratigraphic data whatsoever are available. The fauna from Block "E" bei Nifoekoko contains the following species:

Prenkites timorensis Spath
Eophyllites orientalis Spath
Palaeophyllites steinmanni Welter
Proptychitoides arthaberi (Welter)

Prohungarites similis Spath
Prohungarites crasseplicatus (Welter)
Prohungarites tuberculatus (Welter)
Procarnites skanderbegis Arthaber
Albanites welteri Spath

The *Prohungarites* of this fauna are very similar to the species recorded from southeastern Idaho and suggest a close relationship between these two faunas. The *Albanites, Proptychitoides, Eophyllites,* and *Prenkites* are comparable to species known from Albania (Arthaber, 1911) and the Greek island of Chios (Renz and Renz, 1948). It is the Idaho fauna, however, that gives us the real clue to the stratigraphic position of the fauna from Block "E".

The youngest Scythian zone in the Himalayas is that from the Chocolate limestone at Byans which belongs to the *Anasibirites* zone (Krafft and Diener, 1909). Diener established the existence of two Scythian zones in Kashmir, a lower one belonging to the *Ophiceras* zone and an upper one equivalent to the Hedenstroemia fauna at Spiti. In addition, Diener recognized the possibility of a third zone in the presence of *Prohungarites middlemissi* (Diener). This specimen, however, Diener clearly states came from loose blocks at Pastannah, Kashmir, so that its stratigraphic position is not known. Spath (1934, p. 33) placed this form in his Prohungaritan division at the top of the Scythian.

In the Salt Range, the youngest zone represented by the Ceratite beds (in the Upper Ceratite limestone) is of the *Anasibirites* zone. Above this uppermost fossiliferous horizon, Waagen (1895) recorded a single species, *Pseudharpoceras spiniger*, from the Topmost limestone. Waagen had a single, incomplete specimen from this horizon upon which he established his new genus and species. This form has been largely overlooked since its introduction but Smith (1932) did recognize what he believed to be a conspecific form in the *Columbites* zone of southeastern Idaho. Waagen's specimen is incomplete and weathered but does bear a close similarity to *Hellenites* Renz and Renz (1948) from the Upper Scythian fauna of Chios.

The lower Triassic appears to be well represented in the Karatou Mountains in the Mangyshlak Peninsula (projecting into the eastern Caspian Sea) of southern Russia. This area is especially well known for the presence of *Doricranites* — the type species, *D. bogdoanus* — which was described by v. Buch in 1831. Mojsisovics (1882) subsequently described two additional species. The very unusual nature of *Doricranites* presented a problem as to its correct age assignment but most authors (Mojsisovics, 1882, p. 89; Spath, 1934, p. 382) concluded it was most likely upper Scythian in age. In the meantime, additional forms have been identified from the region with some data on the stratigraphy. Baiarunas (1936) was the first to present a stratigraphic sequence with a list of the ammonites present, which unfortunately include many *nomina nuda*. According to Baiarunas the lowest 15 m. of the Triassic section consist of limestones and marls which contain *Doricranites bogdoanus* v. Buch, *D. rossicus* Mojsisovics, *D. acutus* Mojsisovics, and *Subdoricranites discoides* (*nomina nuda* for both genus and species). It is of interest to note Baiarunas' comment that this fauna was characterized by numerous individuals but few species. Above this lower fossiliferous unit are 100 m. of unfossiliferous siliceous shales. This is followed by 200 m. of marly shales with seams of marly limestone and calcareous marly concretions, rich in ammonites. This series of strata is divisible into four divisions; the lowest part of 23 m. contains *Ophiceras* cf. *demissum*, *Xenodiscus* sp., *Pseudosageceras multilobatum* Noetling, *Neotoceras mokrinskii* Baiarunas (both genus and species *nomina nuda*). The next 30 m. are chiefly characterized by *Pseudosageceras multilobatum* Noetling, *Procolumbites karatauciki* Baiarunas (both genus and species *nomina nuda*), *Procarnites andrusovi* Baiarunas (*nomina nuda*), *Thermalites* n. sp. and other species. The third division of 80 m. contains *Columbites* cf. *parisianus* Hyatt and Smith, *C. asiaticus* Baiarunas (*nomina nuda*), *C. adai* Baiarunas (*nomina nuda*), *C. dolnapensis* Baiarunas (*nomina nuda*), *C. ligatiformis* Baiarunas (*nomina nuda*), *C. tururpensis* Baiarunas (*nomina nuda*), *C. gracilis* Baiarunas (*nomina nuda*), *Tirolites* n. sp. and others (unnamed). The uppermost division of 65 m. is characterized by several forms of *Tirolites* and *Dinarites*.

On the basis of this faunal sequence, Baiarunas (1936) came to the conclusion that since *Doricranites* lay below the beds containing *Pseudosageceras* and *Ophiceras*, the *Doricranites* strata must be correlative with the *Otoceras* beds of the Himalayas, that is, at the base of the Scythian. Each of these faunal assemblages represents a strange mixture of genera normally not found together. This fact plus the large number of *nomina nuda* in the faunal list throws suspicion on the whole study and especially on the conclusions.

Kiparisova (1947) briefly discussed the Mangyshlak section and described some of the ammonites, making specific note of the fact that detailed stratigraphic data were lacking for much of the material available to her. However, she did describe from the upper unit (the 80 m. unit below the uppermost division of 65 m. with *Tirolites* and *Dinarites*) of Baiarunas's section *Columbites dolnapaensis* Kiparisova (= *C. dolnapaensis* Baiarunas MS), *Kashmirites subdimorphus* Kiparisova, *Anasibirites gracilis* Kiparisova (= *Columbites gracilis* Baiarunas MS), and *Tirolites rossicus* Kiparisova.

Recently the stratigraphy of the Mangyshlak region was again briefly reviewed in the volume on the stratigraphy of the USSR by L. P. Kiparisova (1958). Following this author, the Mangyshlak section begins with up to 250 m. of calcareous shales of which the lower 10 m. consists of sandy shale and coarse sandstone with lenses of conglomerate. Above the lower sandy bed the shales contain beds of limestone with abundant ammonoids (*Doricranites bogdoanus* v. Buch, *Tirolites cassianus* Quenstedt, *Procarnites andrusovi* Kiparisova, *Pseudosageceras multilobatum* Noetling, etc.) and pelecypods. Above this are up to 400 m. of argillaceous and sandy shales with interbedded limestone and sandstone. The limestones contain ammonoids (*Columbites* cf. *parisianus* Hyatt and Smith, *Tirolites cassianus* Quenstedt, *Procarnites andrusovi* Kiparisova, *Anasibirites gracilis* Kiparisova, and others) and pelecypods, gastropods and brachiopods. Kiparisova placed these horizons in the upper half of the Scythian.

The incompleteness of these faunal lists, the mixture of genera and species which have not previously been recorded together, and the great thickness of each of the fossiliferous units with no data on the precise stratigraphic relations of the faunas makes interpretation of this section extremely difficult. For one thing, one cannot help but be impressed by the presence of *Procarnites andrusovi* and *Tirolites cassianus* in both of the fossiliferous units. *Procarnites* has previously been recorded from the *Subcolumbites* beds of Albania (Arthaber, 1911) and of Chios (Renz and Renz, 1948). Spath (1934, p. 182) identified specimens in the collections of the British Museum (Natural History) as *Procarnites skanderbegis* Arthaber, from the Nifoekoko locality in Timor (*Albanites* beds). Species of *Tirolites* are best known from the Alpine fauna described by Kittl (1903) and have long been known from southeastern Idaho where they occur in a horizon above the *Anasibirites* zone and below the zone of *Columbites*. Species of *Tirolites* are also known from the *Columbites* zone of southeastern Idaho and from the *Hedenstroemia* beds of the Himalayas (*Tirolites injucundus* Krafft in Krafft and Diener, 1909). No species of *Tirolites* have been recognized in any of the faunas of the *Prohungarites* zone. *Pseudosageceras multilobatum* is world wide in distribution and ranges throughout the Scythian. The specimen identified by Kiparisova as *Anasibirites gracilis* has the appearance of a *Xenoceltites*.

It is apparent from the faunal lists of the Mangyshlak section that several Upper Scythian zones are represented, but until detailed field studies and sections are made and the faunas monographed one cannot evaluate the relationships of these faunas with others of similar age. There is nothing in the specimens known to date from Mangyshlak that shows any affinity to the *Arctoceras* fauna of Spitsbergen.

The Lower Triassic faunas of Djulfa in Armenia are still poorly understood. The best description of the faunas is that of Stoyanow (1910), and the stratigraphy and geology of the region has been well treated by Bonnet (1947). There is a general consensus of opinion that some upper Scythian horizons are represented, but for the immediate purposes of this report it is sufficient to say that the faunas are totally unlike the *Arctoceras* fauna of Spitsbergen.

The upper Scythian faunas of the Mediterranean region need only brief mention. These include the *Tirolites* fauna monographed by Kittl (1903) and the *Subcolumbites* fauna first described by Arthaber (1908, 1911) from Albania and more recently described from the island of Chios by Renz and Renz (1948). The *Subcolumbites* fauna of Albania and Chios is extremely diverse in numbers of genera, many of which show close affinities to the fauna from Block "E" bei Nifoekoko, Timor, and to the *Prohungarites* fauna of southeastern Idaho. The only form in common with the *Arctoceras* fauna of Spitsbergen is the genus *Prosphingites*. However, as mentioned earlier, the species of *Prosphingites* from the *Subcolumbites* fauna of Albania and Chios are very different from the Spitsbergen species or from those species in the *Meekoceras* fauna of western United States.

If one takes into account the composition of all the faunas known from the *Prohungarites* zone (Olenek, Ussuri Bay, Queen Elizabeth Islands, southeastern Idaho, Nevada, Timor, Kashmir, Mangyshlak ?, Djulfa, Chios, and Albania), there are very few forms which could indicate any possible relationship to the *Arctoceras* fauna of Spitsbergen. The *Columbites* and *Tirolites* faunas are known from very few localities and are known in a sequence of faunal zones only in southeastern Idaho. What we know of these faunas likewise does not suggest any close relationship to the *Arctoceras* fauna of Spitsbergen. The relationship of the *Arctoceras* fauna with the zone of *Meekoceras gracilitatus* is based on the close similarity of *Arctoceras blomstrandi* to "*Meekoceras*" *tuberculatum* and to the similarity of *Prosphingites spathi* to the new prosphingitids known from the *Meekoceras* beds of Nevada. However, if it is correct that the *Arctoceras* fauna of Spitsbergen occurs above the *Anasibirites* fauna, then it could not be contemporaneous with the *Meekoceras* fauna of Idaho and it must then represent an additional zone (best considered of Owenitan age) lying above the *Anasibirites* zone and below that of *Tirolites*.

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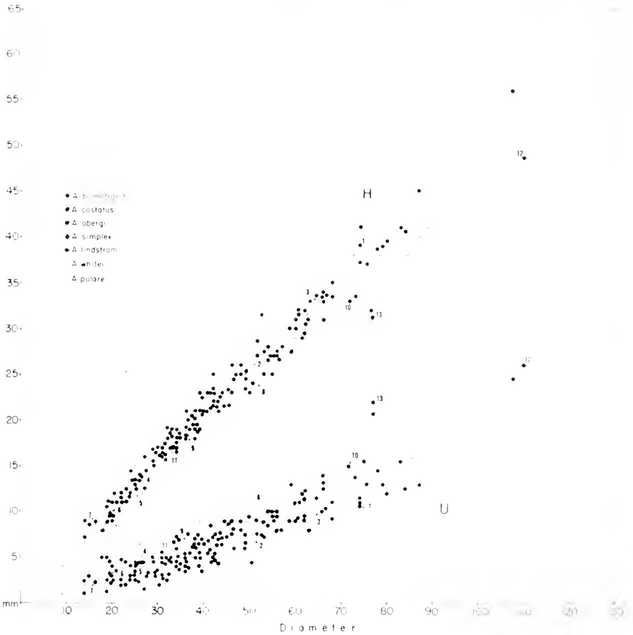
FIGURES AND PLATES

Fig. 1. Height and umbilical diameter of thirteen primary types and of 202 specimens of *Arctoceras* from Spitsbergen in the British Museum (Natural History), identified by L. F. Spath; (141 are specimens labelled *A. blomstrandi,* 41 are specimens labelled *A. whitei,* 11 are specimens of *A. polare,* 8 are of *A. costatus,* and one is *A. öbergi*). The specimens were measured for the author by Mr. Robert Reyer. The number points are the measurements of the primary types of the various species of *Arctoceras.*

1. *A. blomstrandi* (Lindström) NRPAS 247; Mojsisovics, 1886, pl. 6, figs. 8a-c; this report, pl. 1, figs. 1, 2.
2. *A. polare* (Mojsisovics) NRPAS 270; Mojsisovics, 1886, pl. 7, fig. 1; this report, pl. 4, fig. 1.
3. *A. polare* (Mojsisovics) NRPAS 271; Mojsisovics, 1886, pl. 7, fig. 2; this report, pl. 4, fig. 2.
4. *A. simplex* (Mojsisovics) NRPAS 273b; Mojsisovics, 1886, pl. 6, figs. 3a, b; this report, pl. 5, figs. 7, 8.
5. *A. simplex* (Mojsisovics) NRPAS 278; Öberg, 1877, pl. 3, figs. 4a-c; this report, pl. 5, figs. 1, 2.
6. *A. simplex* (Mojsisovics) NRPAS 273c; Mojsisovics, 1886, pl. 6, fig. 4; this report, pl. 5, figs. 3, 4.
7. *A. simplex* (Mojsisovics) NRPAS 273a; Mojsisovics, 1886, pl. 6, figs. 2a, b; this report, pl. 5, figs. 5, 6.
8. *A. whitei* (Mojsisovics) NRPAS 280; Mojsisovics. 1886, pl. 6, figs. 6a, b; this report, pl. 3, figs. 3, 4.
9. *A. whitei* (Mojsisovics) NRPAS 281; Mojsisovics, 1886, pl. 6, figs. 5a, b; this report, pl. 6, fig. 2.
10. *A. öbergi* (Mojsisovics) NRPAS 286; Mojsisovics, 1886, pl. 7, figs. 6a, b; this report, pl. 4, fig. 3.
11. *A. öbergi* (Mojsisovics) NRPAS 284; Mojsisovics, 1886, pl. 7, fig. 5; this report, pl. 5, fig. 10.
12. *A. lindströmi* (Mojsisovics) NRPAS 266; Mojsisovics, 1886, pl. 8, fig. 2; this report, pl. 7, fig. 1.
13. *A. costatus* (Öberg) NRPAS 251; Mojsisovics, 1886, pl. 7, fig. 3; this report, pl. 4, fig. 4.



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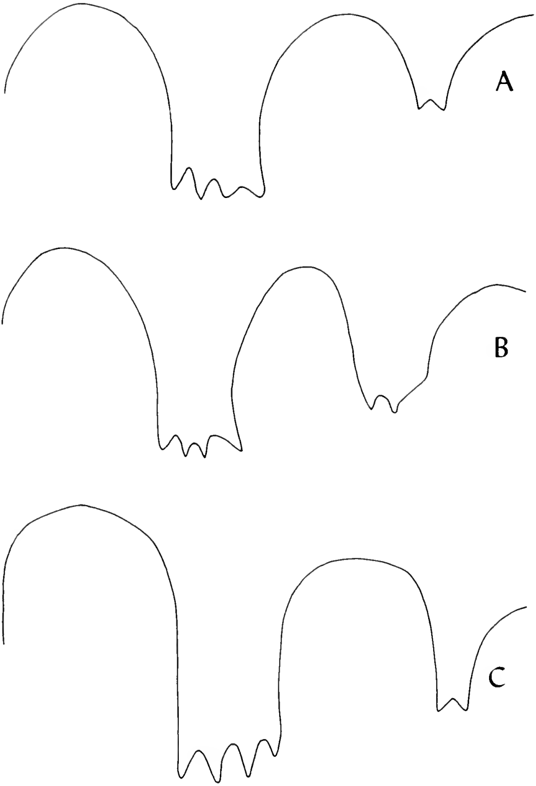

Fig. 2. Diagrammatic representation of sutures of A, *Arctoceras polare* (Mojsisovics), holotype NRPAS 270, X 4.5; B. *A. blomstrandi* (Lindström) holotype NRPAS 247, X 4.1; C, *A. öbergi* (Mojsisovics) holotype NRPAS 289, X 3.2.

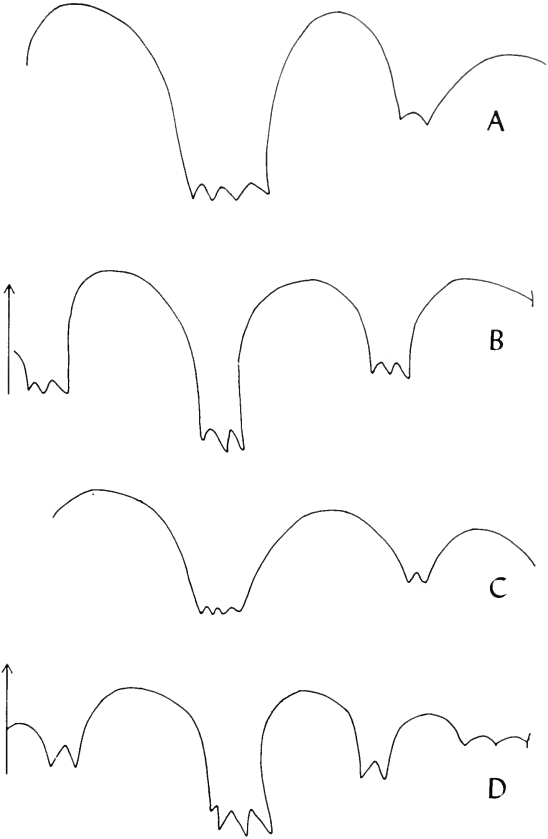

Fig. 3. Diagrammatic representation of sutures of A, *Arctoceras costatus* (Öberg), holotype NRPAS 251, X 4.5; B, *A. lindströmi* (Mojsisovics) holotype NRPAS 266, X 2.8; C, *A. polare* (Mojsisovics) paratype NRPAS 271, X 3.9; D, *A. öbergi* (Mojsisovics) paratype, NRPAS 286, X 2.8.

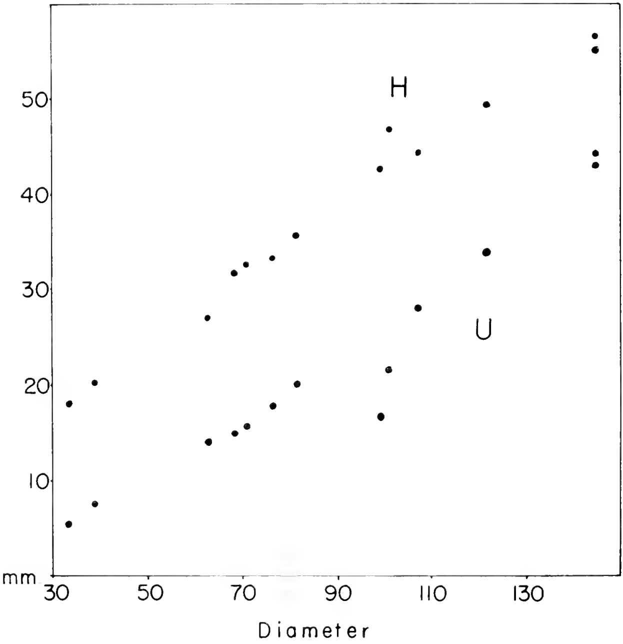

Fig. 4. Height and umbilical diameter of 13 specimens of *Arctoceras tuberculatum* from the *Meekoceras gracilitatus* zone at Crittenden Spring, Elko County, Nevada. Based on specimens deposited in the Museum of Comparative Zoology.

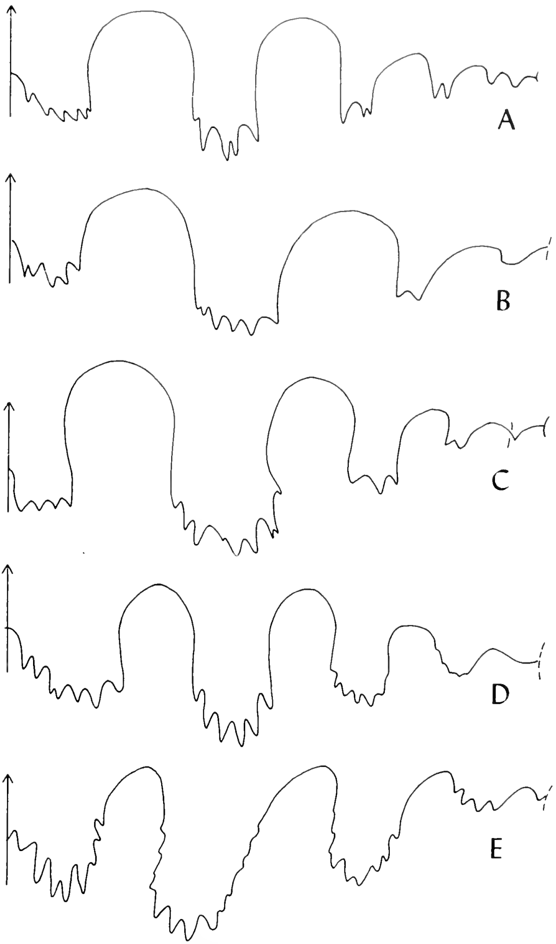

Fig. 5. Diagrammatic representation of the suture of A, *Arctoceras tuberculatum* (Smith) from a large mature specimen, X 2.2; B, *A. tuberculatum* (Smith) from specimen of 34.0 mm. in diameter, MCZ 5325, X 3.2; C, *A. tuberculatum* (Smith) from specimen of 25.0 mm. in diameter, MCZ 5324, X 7.5; D, *A. tuberculatum* (Smith) holotype USNM 74995, X 1.4 (from Smith, 1932, pl. 50, fig. 3); E, *A. tuberculatum* (Smith) paratype USNM 74995, X 1.9 (from Smith, 1932, pl. 50, fig. 4). A-C, from *Meekoceras gracilitatus* zone, Crittenden Spring, Elko County, Nevada. D, E, from *Meekoceras* beds, Union Wash, Inyo Range, California.

PLATE 1. ARCTOCERAS BLOMSTRANDI

Figures

1, 2.	*Arctoceras blomstrandi* (Lindström). Holotype, NRPAS 247, of *Ceratites blomstrandi* Lindström (1865, p. 4, pl. 1, fig. 3; also described and illustrated in Mojsisovics (1886, pp. 29-30, pl. 6, figs. 8a-c) from *Posidonomya* beds, Midterhuk, Spitsbergen. X1.
3, 4.	*Arctoceras blomstrandi* (Lindström). Paratype of *Ceratites blomstrandi* Lindström (1865, p. 4, pl. 1, fig. 4) NRPAS 282, *Posidonomya* beds, Isfjord, Midde Hook, Spitsbergen. X1.

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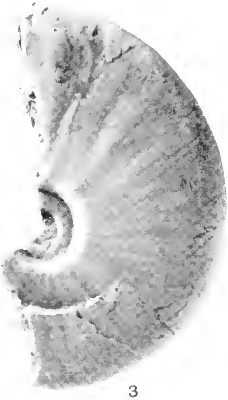

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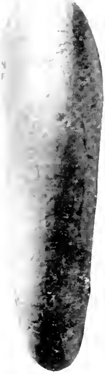

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PLATE 1

PLATE 2. ARCTOCERAS BLOMSTRANDI

Figures

1, 2. *Arctoceras blomstrandi* (Lindström). Two views of holotype of *Ceratites öbergi* Mojsisovics (1886, pl. 8, figs. 3a-b, described and illustrated as *Ceratites blomstrandi* by Öberg (1877, pp. 11-13, pl. 3, figs. 1a-b) from *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen. NRPAS 289. X1.

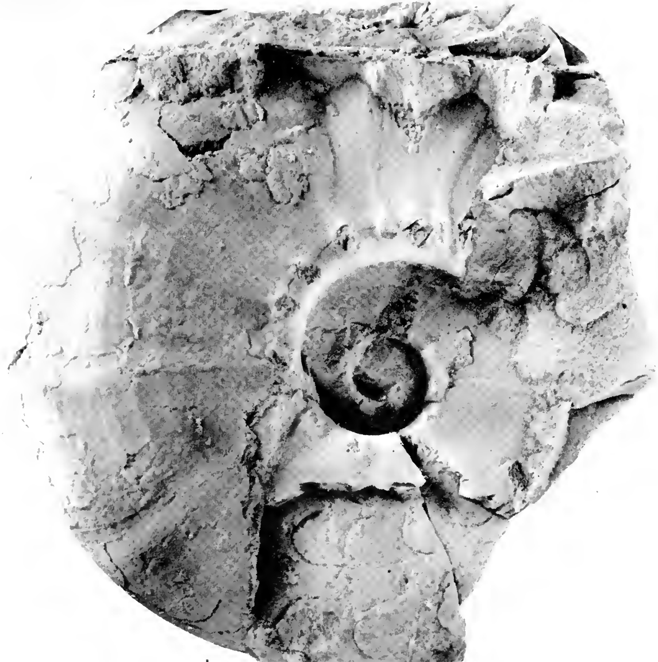

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PLATE 2

PLATE 3. ARCTOCERAS BLOMSTRANDI

Figures

1. *Arctoceras blomstrandi* (Lindström). Specimen identified as *A. polare* by L. F. Spath from Mt. Congress, Spitsbergen, MCZ 6525. X1.
2. *Arctoceras blomstrandi* (Lindström). Figured specimen of *Ceratites* ind. Mojsisovics (1886, p. 32, pl. 6, fig. 7) from *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen. NRPAS 294. X1.

3, 4. *Arctoceras blomstrandi* (Lindström). Two views of holotype of *Ceratites whitei* Mojsisovics (1886, pp. 32-33, pl. 6, figs. 6a-b) from *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen. NRPAS 280. X1.

5. *Arctoceras blomstrandi* (Lindström). Paratype of *Ceratites öbergi* Mojsisovics (1886, pp. 33-34, pl. 8, fig. 1) from *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen. NRPAS 288. X1.

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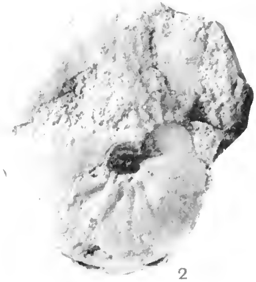

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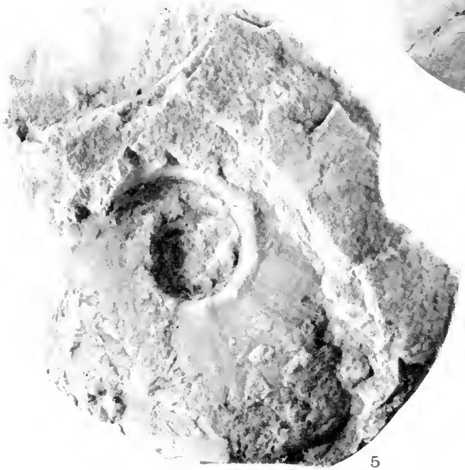

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PLATE 3

PLATE 4. ARCTOCERAS BLOMSTRANDI

Figures

1. *Arctoceras blomstrandi* (Lindström). Holotype of *Ceratites polaris* Mojsisovics (1886, pp. 31-33, pl. 7, figs. 1a-b) first described and illustrated as *Ceratites blomstrandi* in Öberg 1877, pp. 11-13, fig. 3; from *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen. NRPAS 270. X1.
2. *Arctoceras blomstrandi* (Lindström). Paratype of *Ceratites polaris* Mojsisovics (1886, pp. 31-32, pl. 7, fig. 2) from *Posidonomya* beds at Isfjord-Kolonie, Spitsbergen. NRPAS 271. X1.
3. *Arctoceras blomstrandi* (Lindström). Paratype of *Ceratites öbergi* Mojsisovics (1886, pp. 33-34, pl. 7, figs. 6a-b; first described and illustrated as *Ceratites blomstrandi* in Öberg, 1877, pp. 11-13, pl. 3, figs. 2a-b) from *Posidonomya* beds, Isfjord Kolonie, Spitsbergen. NRPAS 286. X1.
4. *Arctoceras blomstrandi* (Lindström). Holotype of *Ceratites costatus* Öberg (1877, pp. 13-14, pl. 1, fig. 3; also figured in Mojsisovics, 1886, pl. 7, figs. 3a-b) from *Posidonomya* beds, Isfjord-Kolonie, Spitsbergen. NRPAS 251. X1.

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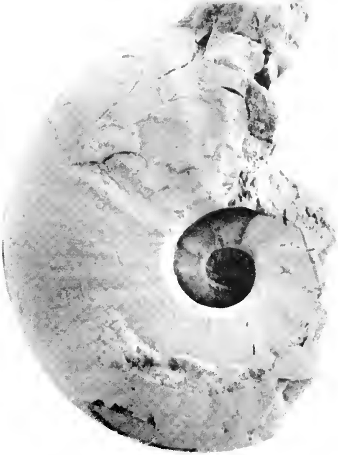

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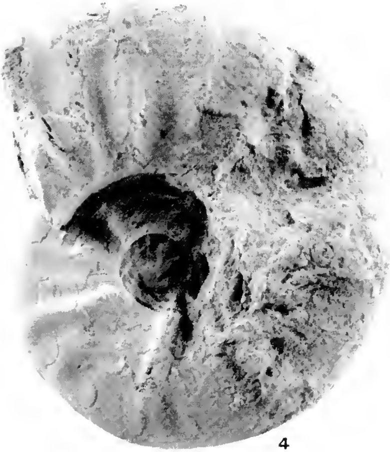

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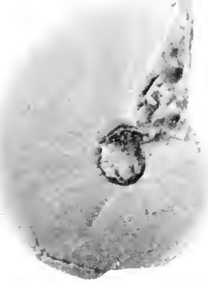
PLATE 4

PLATE 5. ARCTOCERAS BLOMSTRANDI

Figures	
1, 2.	*Arctoceras blomstrandi* (Lindström). Lectotype of *Ceratites simplex* Mojsisovics (1886, pp. 30-31; figured and described as *Ceratites blomstrandi* in Öberg, 1877, pp. 11-13, pl. 3, figs. 4a-e) from *Posidonomya* beds, Isfjord-Kolonie, Spitsbergen. NRPAS 278. X2.
3, 4.	*Arctoceras blomstrandi* (Lindström). Paratype of *Ceratites simplex* Mojsisovics (1886, pp. 30-31, pl. 6, fig. 4-suture) from *Posidonomya* beds, Isfjord-Kolonie, Spitsbergen. NRPAS 273c. X2.
5, 6.	*Arctoceras blomstrandi* (Lindström). Paratype of *Ceratites simplex* Mojsisovics (1886, pp. 30-31, pl. 6, figs. 2a-b) from *Posidonomya* beds, Isfjord-Kolonie, Spitsbergen. NRPAS 273a. X2.
7, 8.	*Arctoceras blomstrandi* (Lindström). Paratype of *Ceratites simplex* Mojsisovics (1886, pp. 30-31, pl. figs. 3a-b) from *Posidonomya* beds, Isfjord-Kolonie, Spitsbergen. NRPAS 273b. X2.
9.	*Arctoceras blomstrandi* (Lindström). Specimen identified as *A. polare* by L. F. Spath, from Mt. Congress, MCZ 6526, X1.
10.	*Arctoceras blomstrandi* (Lindström). Paratype of *Ceratites öbergi* Mojsisovics (1886, p. 33, pl. 7, fig. 5) from *Posidonomya* beds, Isfjord-Kolonie, Spitsbergen. NRPAS 284. X1.



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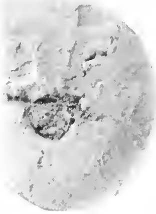

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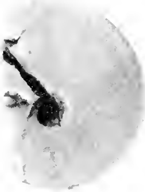

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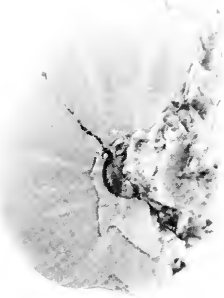

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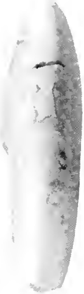

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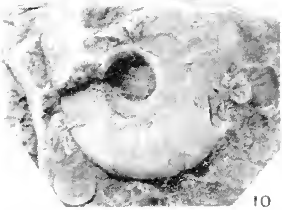

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PLATE 5

PLATE 6. ARCTOCERAS BLOMSTRANDI

Figures

1. *Arctoceras blomstrandi* (Lindström). Suture illustrated by Öberg (1877, p. 14, pl. 4, fig. 1c only); also described and illustrated by Mojsisovics (1886, p. 37, pl. 7, fig. 4) as *Ceratites* nov. f. indet., from Isfjord-Kolonie, Spitsbergen. NRPAS 293. X1.

2. *Arctoceras blomstrandi* (Lindström). Paratype of *Ceratites whitei* Mojsisovics (1886, pp. 32-33, pl. 6, figs. 5a, b) from *Posidonomya* beds, Isfjord-Kolonie, Spitsbergen. NRPAS 281. X1.

3, 4. *Arctoceras blomstrandi* (Lindström). Plesiotype from *Posidonomya* beds, Spitsbergen. NRPAS 2383. X1.

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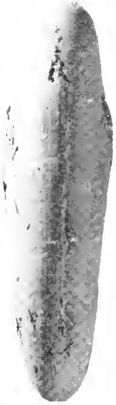

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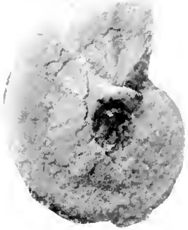

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PLATE 6

PLATE 7. ARCTOCERAS BLOMSTRANDI AND TUBERCULATUM

Figures	
1.	*Arctoceras blomstrandi* (Lindström). Holotype of *Ceratites lindströmi* Mojsisovics (1886, p. 35, pl. 8, fig. 2) from *Posidonomya* beds, Isfjord-Kolonie, Spitsbergen. NRPAS 266. X1.
2, 3.	*Arctoceras tuberculatum* (Smith). Plesiotype from *Meekoceras gracilitatus* zone, Crittenden Spring, Elko County, Nevada. MCZ 6527. X1.

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PLATE 7

PLATE 8. ARCTOCERAS TUBERCULATUM

Figures	
1, 2.	*Arctoceras tuberculatum* (Smith). Holotype from *Meekoceras* beds, Union Wash, Inyo Range, California. USNM 74995, X0.5.
3-5.	*Arctoceras tuberculatum* (Smith). Plesiotype from *Meekoceras gracilitatus* zone, Crittenden Spring, Elko County, Nevada. 3, MCZ 5322, X1; 4, 5, MCZ 5324, X1.


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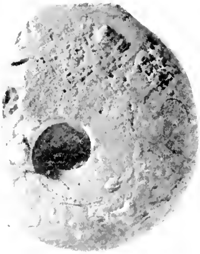
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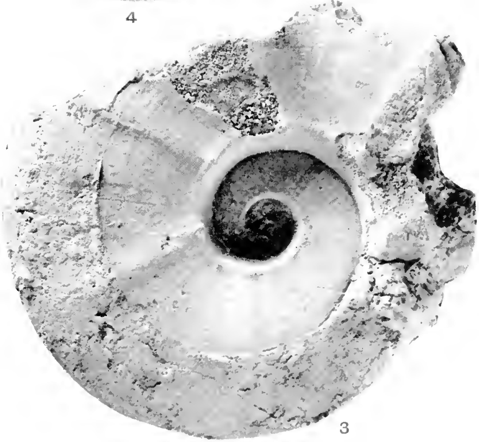
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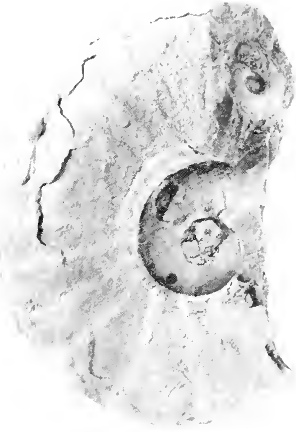
PLATE 8

PLATE 9. ARCTOCERAS TUBERCULATUM

Figures

1-5. *Arctoceras tuberculatum* (Smith). Plesotypes from *Meekoceras gracilitatus* zone, Crittenden Spring, Elko County, Nevada. 1, MCZ 5320, X0.5; 2, MCZ 5321, X0.5; 3, MCZ 5323, X1; 4, 5, MCZ 5325, X1.



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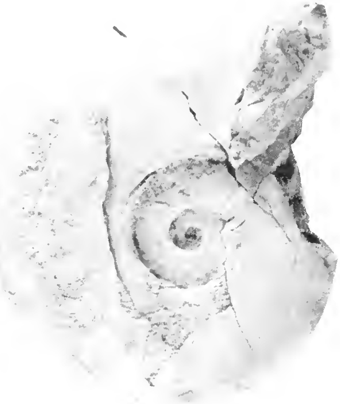

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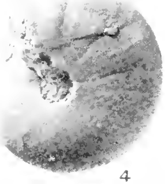

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PLATE 9

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