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AGE CHANGES IN THE PUBIC BONE

V. MAMMALIAN PUBIC METAMORPHOSIS

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INTRODUCTION

In the earlier part of this work the results obtained repeatedly impressed one with the possibility of expanding the linkages of pubic metamorphosis to include not merely Sex and Stock but also Family, Order and Class. For example in the section upon Stock-linked characters (28 p. 49) attention was drawn to significant differences between White and Negro-hybrid Stocks. In the White there is frequently an ill-marked condition or even almost total absence of the ridge and furrow system of the symphysial face and also a very great tendency to have the ventral margin formed by gradual accretion of bone tissue instead of by a series of isolated bony nodules fusing to form bridges and later a definite rampart. In the Negro-hybrid the ridge and furrow system is much more constant and though in some cases the ventral margin is formed by simple accretion the rampart is noticeably frequent and in occasional exceptions (e. g. No. 744, see 28 Part II, p. 17) appears abnormally early. The question naturally arises as to what course in metamorphosis is the more typical of the order to which Man belongs. Does the condition in the White represent a deviation or is the Negro-hybrid progressive. One no sooner opens the problem of the Primate symphysis than one inquires what is the relation of this symphysis to that of other mammals. Whereas the os pubis of reptiles has received considerable attention the more immediate problem of the mammalian bone seems to have suffered neglect.

The stability in general of the pubis is a question well worth inquiring into. The bone bears an intimate relation in position to the sex organs which, as is clearly recognized, possess great value in the study of phylogeny. How stable the os pubis actually is in the Class Mammalia will appear later in this work.

A third question prompted by the Stock-linked characters of this bone is that of its relation to habit. In skeleton investigation one is often tempted to believe that too much has been assumed as to the effect of the erect posture in Man and that, with further investigation upon a more abundant material, some of the so-called results of the erect posture will be found to be typical mammalian age changes. One is impressed with the uniformity and the adherence to type of the mammalian skeleton in general.

It is apparent from the above sketch that no investigation of the human os pubis would have been complete had this section of the work

not been undertaken. And as we shall discover very quickly it would be impossible otherwise to grasp the significance of the variations in the human bone to which allusion has just been made.

MATERIAL—THE HAMANN MUSEUM

One of the most serious drawbacks to systematic work of the kind represented in this memoir is the scattered condition and relative inaccessibility of necessary collections upon which the investigation can be made. There are now in many of the great Museums vast collections of mammalian material suitable for study. Rarely can one obtain in the same Institution a corresponding collection of human skeletons in such order that individual bones can be assembled with speed and accuracy. A relatively small collection of mammals, provided it be fairly representative, and of human material, if properly prepared for systematic study, so that the worker can live with it day after day instead of having to make comparisons by memory, gives a most effective opportunity for these investigations.

In 1893, Dr. C. A. Hamann, then newly appointed to the Chair of Anatomy, conceived the plan of forming a Museum in which the normal and abnormal in human structure might be studied from clinical and comparative aspects alike. This vision led Dr. Hamann to gather and to prepare specimens upon Hunterian principles, so that in course of time there grew up in Cleveland a Museum similar in scope if not in extent to the collection formed by John Hunter. As Dr. Hamann's time became more encroached upon by practice he gave correspondingly generously in funds for the carrying out of his ideal. As one to whom there has come the privilege of assisting in the realization of this ideal and the unique opportunity of working among its treasures, I feel it fitting that acknowledgment be made at this time and at this stage in the presentation of our results. The great value of the Hamann Museum of Comparative Anthropology and Anatomy of Western Reserve University, as a center for research, must speedily become known.

It is not my intention here to dilate upon the Museum as a whole or to give an account of what has been rendered possible by the generosity of the Trustees in further financing the Department to take the fullest advantage of Dr. Hamann's gifts. I have previously mentioned the collection of human skeletons; I would now state merely that to a large extent the comparative material, both in the fresh state and as skeletons, has been gathered with especial care as to data. The skeletons are housed exactly as are the human skeletons, and every bone likewise

bears the catalogue number of the skeleton to which it belongs. Every arrangement has been made so that this collection is equally accessible with the human skeletons for comprehensive and intensive study. So far there are nearly seven hundred mammalian skeletons and skulls besides a large number of fresh examples still in the hide with which, however, we have no particular interest in this memoir.

LIFE PERIODS

In this work on pubic metamorphosis there are two distinct parts. In the first place we are investigating the changes which the symphysial region undergoes and in the second we are checking up these changes against time. So far as the human material is concerned it is convenient and quite intelligible to compute these changes in years. We understand perfectly well at what stage of his life period and in approximately what physical condition a human individual is likely to be if we know his age in years. The moment we begin to discuss other forms of life, however, our time standard fails us. Not only is the total period of life for almost all other animals at best very imperfectly known but the successive stages of the life period bear quite differing relations to time. Yet if we are to make any useful comparison between Man and other animals there must be some common life standard upon which the comparison may be based.

In his memoir on the Rat Donaldson (7. p. 6) makes the following statement. "The comparison of the experimental results obtained on animals with the corresponding results on man has heretofore been difficult because of the absence of a good basis for comparison. We have found reason to assume that in the case of the rat the post-natal span of life of three years is approximately equivalent to the span of ninety years in man or to put it another way, that the rat grows thirty times as fast as man. This ratio appears to hold for fractions of the span, as well as for the entire span. All of the data for the Albino, based on postnatal age, may therefore be compared fairly with the corresponding data for man." If this statement in its entirety were upheld we should be in a position to compare time relationships in skeletal metamorphosis in the Rat and in Man provided we knew exactly the age of the rat skeletons under observation. In the case of other animals we might also make the comparison provided the same information were available and in addition we knew the approximate post-natal span of life. The exact age of an individual is likely to be known in only very few animals, and these certainly not wild ones.

The approximate life span may eventually be known but there are no data available now. Chalmers Mitchell (20) has pointed out how extremely inadequate are any data existant on this subject for purposes of correlation, and further, how unwise in general it would be to assume that the life span of an animal in captivity is that of the same species in the wild state.

We may also rule out as ingenious speculations, or at best theories of no practical significance, the successive expositions from Bacon to Metchnikoff upon the relation of the life span to some particular feature of growth or structure or function. These are admirably reviewed in Mitchell's work and require no further presentation.

It appears certain that if we should have all the information called for in the two foregoing paragraphs we should even yet have no effective standard for comparison between different animals. Four years after the statement already quoted Donaldson (8 p. 301) shows that the total life span presents certain difficulties as a basis for comparison. In a discussion of skeletal growth there occurs the following significant paragraph.

"Our records do not show just how long the growth of the skeleton in weight continues in the rat, but from the data at hand we should say it was still growing at 474 days of age, which, according to our usual computation (Donaldson, '15, p. 6) is equivalent to thirty-nine years of human life. The only datum for man with which this can be compared is the linear measurement represented by the stature, which seems to reach its maximum at about twenty-eight years in the human male and twenty-five years in the female. If the increase in the weight of the human skeleton ceases at the time when the increase in stature stops, then it is clear that the growing period for the skeleton of the rat is much longer continued, and this conclusion agrees with our general impressions concerning the growth of this animal." If this be true then the total life span is of little value in comparing phases of metamorphosis in the skeletons of different animals.

The only other specific information now available relative to age changes in the mammalian skeleton apart from the usual epiphysial features has been reviewed by Donaldson (8 p. 303). It is extremely fragmentary in scope, indefinite in time relation, and largely confined to statements of senile changes. R. M. Strong, on the other hand, is at the moment engaged on a work of great importance. Only a preliminary communication has so far been published (25), but from this it

is plain that Strong's investigation will enable exact comparisons to be made in the skeletal growth of Man, the Rat and certain birds.

Having thus exhausted every possibility of obtaining an accepted standard for comparison of skeletal metamorphosis in different mammals it became necessary to devise a method, which, however much it may ultimately have to be modified, will at least enable us to proceed with comparisons of age-relationship of skeletal metamorphosis. The absence of any standard has resulted in adoption of various arbitrary subdivisions of the life period based upon assumptions easily shown to be untenable. I do not here refer so much to the earlier period of life in which fusion of epiphyses on the long bones takes place, although our studies indicate ultimate modification of existing impressions even on this subject. I do not refer either to the terminal period of life when obviously senile features are present, but rather to the period between these two extremes. Closure of the cranial sutures, for example, is one favorite method of determining age. Parsons has thrown doubt upon the validity of this method (22), and a forthcoming publication from this laboratory amply bears out Parsons' contention. One has only to examine a series of skulls of Gorilla and Man to observe how futile must be any comparison of relative age-period based upon closure of cranial sutures. The eruption of teeth is so notoriously diversified in its relation to age that it does not even merit mention. It is unnecessary to review further standards already obsolescent.

In formulating a scheme for comparison of skeletal metamorphosis it is obviously advantageous to select standards which, although themselves skeletal, bear some general relation to the animal as a whole. They must also be features which are relatively little affected in appearance by environment, habit or morphological relationship. They must be general in their occurrence throughout the series to be compared. For this investigation they must be common to all mammals. It is not an easy thing to pick out a series of features conforming to this exacting standard and occurring at intervals throughout the total life period. We have reason to believe, however, that the limits outlined in the ensuing table have sufficiently stable relationship to the general life (not necessarily to the total life period) of the animal to serve as a framework upon which other features of skeletal metamorphosis, more variable in their age incidence, may be plotted out.

LIFE PERIOD	IN MAN	LIMITS (27).
I.	0-12 years	Terminates in union of acetabular elements.
II.	12-20 years	Terminates in union of long bone epiphyses.

III.	20-24 years	Terminates in union of epiphyses of centra.
IV.	24-36 years	Terminates with appearance of lipping of limb bones.
V.	36-50 years	Commences with this lipping and terminates with the appearance of senile (quasi-pathological) erosions and osteophytic growths at joints, and with the occurrence of senile textures of bones.
VI.	50- years	Commences with the appearance of the irregular features just mentioned.

Each of these features merits a full discussion and in the course of time it will become necessary to make an intensive study of them. But for the present we use these characters in an experimental manner to test their value. Later it may be found possible to expand the table and make it more complete; it may be necessary to modify it by withdrawing certain features and substituting others. In other words this table is tentative and preliminary. It is used as a proving ground for other age changes and if it prove a poor proving ground another can be substituted. The reader must not get the impression that it is permanent or immutable.

In the table I have inserted the corresponding age limits for Man to show that the periods are by no means equal in their time relationship. If periods II and III be merged as one there is a fair spacing out so far as the human life span is concerned. It would certainly be premature in the present fragmentary state of our knowledge, to assume that there is of necessity even an approximately similar subdivision of the total life span of every mammal: it may be so but proof is not yet forthcoming. Because it is particularly important that no preconceived notions creep into the work I have refrained from making any attempt to space out the life span at all equally. Hence I regard it as essential to retain periods II and III as separate intervals.

As we work through the series of mammalian pelves upon which this study is based we shall refer each to its particular life period so that there may be some way in which we may roughly compare one animal with another in respect to the position of each individual relative to the life cycle of its own species.

HISTORICAL REVIEW

Metamorphosis in the region of the mammalian pubic symphysis as an age change has never received any attention so far as I have been

able to find. The morphology of the area, on the contrary, has led several investigators to lay down theories, some of which, though strictly beyond the scope of this work, nevertheless should be noted. In a series of articles Mehnert (16, 17, 18, 19) published a number of striking findings relating to the os pubis of vertebrates. Like most authors Mehnert's interest in the pubis was secondary to his desire to elucidate the pelvis as a whole. He is therefore concerned more with the reptilian pelvis than with that of mammals and in discussing the symphysial area it is the problem of the epipubis and the hypoischium which absorbs most of his attention.

In brief Mehnert was concerned with the morphology and fate of three structures, the epipubis, the ligamentum medianum and the hypoischium, lying in this order antero-posteriorly in the ventral median line of the vertebrate pelvis. Hoffmann had claimed a single median origin for the os hypoischium; Fürbringer on the contrary declared it to be bilateral originally. Mehnert in his general work upon the pelvis had investigated reptiles, birds and mammals and as the results of his investigation strongly supported Fürbringer. In his final article, with the whole of his previous experience to give maturity to his judgment, but referring particularly to the Sauria, Mehnert (19) summarizes his views in a statement of vital importance for the correct appreciation of the investigation upon which we are now engaged. I therefore quote this summary in full.

"Das Hypoischium entsteht durch Verschmelzung zweier, an den Endabschnitten der Ischia in Erscheinung tretender Zellhöcker. Anfangs steht die Cartilago hypoischium mit den Ischiis noch in einem kontinuirlichen knorpeligen Zusammenhange, welcher später schwindet durch Ausbildung einer trennenden Bindegewebszone. Das Hypoischium zeigt bei ausgewachsenen Exemplaren der verschiedenen Landsaurierspecies sehr grosse Formverschiedenheiten. Bei einigen Formen ist es ungleich rautenförmig, bald mit spitzwinkeligen, bald mit abgerundeten Ecken versehen, so dass selbst eine dreieckige Gestalt resultiren kann; bei anderen repräsentirt es die Gestalt eines Stabes, welcher entweder kurz oder lang, dick oder schmal sein kann. Das der Kloake zugekehrte Ende des Hypoischium läuft mehr oder minder spitz zu oder entsendet zwei divergirende Fortsätze. Auch die Verbindung des Hypoischium mit den Ischiis kommt auf verschiedene Art zu Stande. Bald ragt das Hypoischium mehr oder weniger tief in die Symphysis ischii hinein; bei anderen ist dieses Ende abgerundet. Wieder bei anderen trifft man zwei Fortsätze, welche divergirend mit den Ischiis in Berührung treten. Wie auch immer das Os hypoischium gestaltet sein mag, die grösste Konstanz der Beziehungen lässt stets das Ligamentum hypoischium erkennen. Beim individuellen Fehlen eines Os hypoischium vertritt seine Stelle das Ligamentum hypoischium. Diese Inkonstanz des Os hypoischium bei ausgewachsenen Landsauriern lässt es als durchaus wahrscheinlich erscheinen, dass dieses Knochenelement, eben so wie bei der Emys lutaria taurica die Cartilago hypoischium, ein in der Rückbildung begriffener Skelettheil ist.

"Das Epipubis entsteht gleichfalls durch Konfluenz zweier an den Endabschnitten der Schambeine sich ausbildenden Zellhöcker. Anfangs lässt das Epipubis in seiner mehr caudal gelegenen Partie noch einen medianen Spalt erkennen, welcher später zur Verwachsung gelangt. Der ursprüngliche knorpelige Zusammenhang mit den Pubis wird gelöst durch das Auftreten einer trennenden Bindegewebszone. Dieser bei Lacerta eruirte Entwicklungsmodus stimmt mit dem bei Emys lutaria taurica und von A. Bunge bei Triton cristatus beobachteten Verhältnissen überein.

"Dem Ligamentum medianum pelvis kommt bei Lacerta vivipara keine skeletovikarirende Bedeutung zu. Es entsteht in loco nach Art eines intermuskulären Bindegewebsseptum und hängt mit diesem auf das innigste zusammen. Die Beziehungen des Ligamentum medianum zum Beckengürtel müssen daher als sekundäre gedeutet werden.

"Sämmtliche in der ventralen Medianlinie gelegenen Gebilde: das Epipubis, Ligamentum medianum und Hypoischium treten ontogenetisch später in Erscheinung als die beiden primären Beckengürtelhälften, dokumentiren somit in diesem Verhalten das unverkennbare Gepräge von Sekundärbildungen.

The essence of this statement for us is that along the caudo-mesial margin of the pubis and ischium there develops a series of secondary ossifications which already in modern reptiles is prone to retrogression. Although his work on the mammals was mostly upon embryos Mehnert could not fail to be impressed with the appearance presented by the adult animal. He states (18) that a hypoischial-like bone occurs in the following lower mammals: Macropus, Petrogale, Perameles, Didelphis, Pholidotus and Castor. In other mammals and in Monotremes Mehnert failed to discover such a bone. The detailed consideration of the significance of this observation which is promised in the future I have failed to locate. Later we shall see that Mehnert might with advantage have carried this investigation much further.

It is curious that Mehnert should deny to the lig. med. pelvis any morphological relationship to the skeleton of the pelvis. This is critized by Howes and Swinnerton (14) who point out that Wiedersheim described a cartilaginous tract in the adult Sphenodon continuous uninterruptedly with the epipubis and hypoischium. Howes and Swinnerton show that Wiedersheim's statement is an error for although there is such a cartilaginous tract originally it is already replaced by the ligament before hatching (stage R.). It would seem that Mehnert is incorrect in making such a distinction for the ligamentum medianum.

That specific ossifications occur in the tissue along the conjoint rami of pubis and ischium has long been known. Owen (2) in 1866 described a triangular ossicle wedged between the ischia just caudal to the symphysis in a young Potorous. Albrecht (1) in 1883 noted the occurrence of an "interpubic bone" in Edentates. In 1886 Anderson (2) found

Owen's triangular ossicle in a "kangaroo," in Phacochoerus and in Castor and definitely homologized it with the os cloacae (hypoischium) of lizards.

No real attempt was made however at a systematic investigation of the mammalian pelvis from this point of view until Parsons undertook it in 1903 (23). Parsons was stimulated by the work of Mehnert and examined the great collections in the British Museum and the Royal College of Surgeons. He misunderstood Mehnert's position and misquotes him. It will be noted that Mehnert does not state, as Parsons make him do, that epipubis and hypoischium are formed in the mid-line and are at first independent of the rest of the pelvis, but just the contrary.

Parsons discusses symphysial metamorphosis in Kangaroos and does not believe that in these animals the hypoischium ever unites with the rest of the pelvis. He considers the ossification as probably of bilateral origin. In Ornithorhynchus epipubis and hypoischium occur but fuse early. In Rodents and Ungulates the hypoischial element is quite distinct and the symphysis ischio-pubic but ossification in the hypoischium is bilateral and the two parts do not unite. Hence no triangular bone is formed as in Macropus. The inadequacy of these results clearly indicates the truth of my contention that a small representative collection efficiently arranged is of more service in investigation than a large collection in which the correlations have to be made by memory. Nevertheless Parsons leaped to the real significance of the features which he was considering and, even upon the meager human material at his disposal in London, made a true comparison with the features of the human pelvis. In this as in so many other problems, especially those connected with physical anthropology we have to acknowledge Parsons as a real pathfinder, and one who by his efforts and by pointing out the difficulties he encountered, has smoothed the way for those who follow after.

The Reptilian Symphysis

As it is not intended to discuss the morphology of the symphysial region except as it relates to the differentiation shown in modern mammals we shall first consider the condition in the Monotremes as illustrative of the reptilian affiliation.

So far as the reptiles go Sphenodon is a convenient starting point. Our single specimen gives no further information than the excellent figures in the memoir by Howes and Swinnerton (14) to which the reader is referred. Plate VI Figs. 7, 8, 9, and text Figs. 13 and 14 depict the pelvis in the embryonic and the adult state. From Figs.

13 and 14 one notes that the pubis and ischium do not form a continuous symphysial area and are separated from their fellows of the opposite side by an antero-posterior series of elements, namely the epipubis, median ligament and hypoischium. These three in the earlier stages form one continuous tract of cartilage but even before hatching the middle portion has become transformed into the ligamentous tissue of the median pelvic ligament. Neither epipubic nor hypoischial cartilage becomes ossified or shows any indication of an originally bilateral origin. I believe this single median appearance of the three elements is a secondary condition in view of the work of Mehnert. Our observations on the Mammalia thoroughly bear out such an opinion. In Sphenodon there is an epiphysis for the ischial tuber limited to the tuber itself.

Mammalian Pubic Metamorphosis

Mammalian pubic symphyses may be subdivided into three groups.

1. Those in which the two pelvic halves ultimately fuse together at the symphysis.

2. Those in which, as in Man, the two pelvic halves remain separate throughout life but which articulate together by symphysial bony surfaces.

3. Those in which the two pelvic halves do not meet at the symphysis but either are united with each other simply by a ligamentous band, the bony surfaces not touching, or are more or less widely separated and have no connection at all.

These three types bear no relation to the various orders of mammals. One would naturally turn first to the Monotremes and Marsupials and then to the Rodents and to the Insectivores with their close relations the Dermoptera and Chiroptera for information regarding the symphysis. As a matter of fact one finds that all modern examples of the two first-mentioned orders possess a symphysis of the first type and in the other group all three types are found. In the Rodentia and Insectivora there is great variation in the symphysis and in some animals a very notable specialization. Chapman (6) has recently dwelt upon this topic and it is unncessary therefore to do more than outline his facts. In both orders three groups of pelvis are found. In the first group the pubic symphysis is rather long and represents the general mammalian condition. In the second, owing to divergence cranially or caudally of the structures entering into this formation, the symphysis is short, often extremely so. In the third the symphysis is entirely absent in consequence of the failure of the two halves of the pelvis to meet in the middle

line. The reader will note that the slight distinction between Chapman's groups and my types results from the fact that he was concerned with the two orders Insectivora and Rodentia alone, whereas my types cover the entire mammalian Class.

The reason for the marked differentiation of the symphysial region at once attracts attention but we are not yet in position to state why one form should occur rather than another. Chapman, it is true, attempts to correlate his third group with pronounced burrowing but with this view I am not in accord. The condition in Edentates and in certain other mammals such as the Phocidae, Dermoptera, Chiroptera and even the rodent Coendou seems to indicate the unwisdom of drawing specific conclusions as to any true correlation with the burrowing habit. Chapman's work is especially valuable in showing the progress of specialization through his second group to his third in the Pocket Gophers and in emphasizing the lack of any precise taxonomic value in the symphysial region.

In view of the great difficulty of obtaining the precise stages necessary to present the full history of pubic metamorphosis it will be impossible to arrange the material in acceptable phylogenetic order, and no effort will be made to follow any established phylogenetic scheme except in a very general manner.

Also, for the sake of such brevity as may be compatible with a proper presentation of the evidence, only those specimens which are of particular value in the argument will be presented.

MONOTREMATA

For the relation of the mammalian pelvis to that of the reptile various articles by Seeley (e. g., 24) and Broom (e. g., 4, 5) should be consulted. The plate-like formation of the combined pubes and ischia of the Permian reptiles is retained by the Monotremata (Gregory, 11 pp. 115, 154). There is a marked distinction between the pelvis of the Monotremata and that of the Marsupialia, much greater indeed than that between the pelves of a Marsupial and of a menotyphlous Insectivore.

When we attempt to refer the Monotreme skeletons to their respective life periods it appears that the arrangement of life periods presented in a former section of this paper breaks down. The Monotremata possess no epiphyses on the centra of the presacral vertebrae. This is probably a secondary condition as Gregory points out (11 p. 152) but it nevertheless removes from consideration life period III so far as

the Monotremes are concerned. The above arrangement of life periods was made for the Eutheria however and for these it holds pretty well. In what stage relative to the total life span or to the life in general the limb epiphyses fuse in Monotremata I do not know but there is at present no sufficient evidence to indicate that this differs very much from the corresponding stage in the Eutheria.

Ornithorhynchus anatinus B 174, is an animal before the limb epiphyses have fused. No epiphyses are to be seen on the centra of the sacral vertebrae. This is undoubtedly a young animal and its pelvis shows no fusion as yet of the successive sacral vertebrae or of ilia with sacrum. The symphysis (Fig. 1) is ischio-pubic. There is a broad mass of bone between the symphysis and the obturator foramen. No ossification has occurred in the symphysis. The epiphysis for the ischial tuber is ossified but not fused; it is limited to the tip of the tuber and does not extend along the ischial ramus.

Echidna aculeata B. 175 (Fig. 2), is in the same period of life as the foregoing specimen but is a considerably older animal for the sacrum is now a single bone fused on each side with the ilium. The symphysis is also ossified. For convenience we may assume that it is in the second life period. Again the epiphysis for the ischial tuber is unfused. Though it is lost from this specimen the ischial ramus on close examination shows clearly that the epiphysis extended about half way along the margin of the ischial ramus, which fact is confirmed by the following skeleton. A great change from the symphysis in B 174 is apparent. The suture between pubis and ischium on each side has disappeared and the symphysis itself is completely ossified so that the entire pelvis forms a single mass. Heaped on the front of the symphysis in the median sagittal plane is a crest of newly formed bone. Looked at with a dissecting microscope this appears to have developed independently of the pubis and ischium and to have fused with these elements secondarily. It expands at both its cranial and its caudal extremities and sinks in between the two pubes and the two ischia at these points. It is upon this peculiar dumb-bell shaped mass of bone that most of our attention will be focused.

Echidna aculeata, B 547, is an older animal; it is in the fourth life period. That is to say all epiphyses are fused and lipping at the joint surfaces has not yet appeared. Its symphysis bears out strikingly the features described for B 175. In spite of fusion of the epiphysis for the tuber and at the symphysis the former plainly extends half-way along the ischio-pubic ramus and in front of the latter is the separately

ossified bony rod, now one with the pelvis itself but shaped exactly as in B 175.

In the Monotremes we observe that ossification at the symphysis is completed by the appearance of two median wedges of bone, one at each extremity of the symphysis, cephalic and caudal. We note further that these two bony wedges are connected by a median bony bar lying rather on the ventral aspect of the symphysis but as in the case of its wedge-like extremities ultimately, fusing with the symphysial part of the pelvis. This median dumb-bell shaped ossification, like the corresponding fibro-cartilaginous mass in Sphenodon and other reptiles, although extremely ancient, is a secondary condition in all probability.

MARSUPIALIA

Altogether nineteen skeletons of Marsupials have been examined with special reference to the symphysial region, comprising all existing families and sub-families except the Myrmecobiidae, Tarsipedinae, and Phascolarctinae which are represented by skulls only in the collection as yet.

In accordance with our general method the age of these skeletons is recorded by reference to special phases of the life period. In the Marsupial the two halves of the pelvis are already fused at the pubic symphysis before the epiphyses of the long bones have united with the shafts, that is to say before the end of the second life period. The same condition was found in the Monotremes.

As regards dentition the fourth molars were already erupted in all specimens examined and here recorded with the exception of certain Macropodidae in which, as is well known there is considerable retardation in eruption of the distal molars. The exceptions then are the three following in order of age recorded by teeth and pubis.

B 192 Petrogale xanthopus in which the milk molar is still in position and M. 3 is just erupting:

B 182 Macropus bennetti in which M. 4 is appearing above the alveolus:

B 181 Macropus bennetti in which M. 4 is almost in position.

As already indicated no precise phylogenetic order will be followed in presenting the Marsupialia. In any case this would be unnecessary since all marsupial pubic regions are fairly uniform and typical, displaying a symphysis of pubic and ischial parts, so far as our collection goes, except in Notoryctes our specimen of which (B 134) is too old

to give any help in the present work. We shall consider the Diprotodontia first.

The first specimen is Petaurus breviceps B 187 (Fig. 3). This animal is in the second life period, namely before the union of long bone epiphyses. Intervening between the symphysial faces of the two pelvic bones is a long slender dagger-shaped disc of bone, having a slight expansion above and bifurcating at its lower extremity to become continuous with the epiphyses running back to the ischial tubera. Examined from the back the two pelvic bones approximate each other, leaving merely a slightly widened gap above for the enlarged upper end of the median disc but separating widely below to admit the triangular lower end of the median disc which is plainly seen. Only the lower end however is visible from behind. The important features of this specimen are the following.

Ossification is continuous in the tissue along the ischio-pubic ramus from ischial tuber to upper end of pubic symphysis.

The ossification forms a single median bar of bone throughout the symphysial area in which the ischia share as well as the pubes.

It consists of expanded upper and lower extremities and for the most part, forming a wedge between the pelvic bones, does not extend through the entire symphysis from front to back. As previously mentioned, the enlarged lower extremity alone is visible from behind although there is a slightly widened gap at the upper end of the symphysis.

Three specimens of Phascolomys give important information on the method of ossification of the median disc and its ultimate fate. The first of these, Phascolomys tasmaniensis B 183 has not yet attained fusion of the three acetabular elements. Here is merely a cartilaginous union at the symphysis, the cartilage in the fresh state extending along the ramus to each ischial tuber. The symphysial face is somewhat wider in its upper or pubic portion but both pubic and ischial symphysial faces show typical horizontal ridge and furrow formation.

The second specimen, Phascolomys tasmaniensis B 601 (Fig. 4), is of the second life period before fusion of the long bone epiphyses. Ossification has taken place in the cartilage along the ischial tuber but does not yet extend along the ramus. There is a small bony nodule in the cartilage at the lower end of the symphysial area. This we shall call the lower nodule. A second small ossification occurs immediately above this but nowhere else is the median disc transformed into bone. There is a difference in the apperance of the upper, wider symphysial face in that its ridges are larger and more irregular. A dorsal margin is developing at upper and lower extremities of the symphysial face.

The third specimen, Phascolomys latifrons B 602 (Fig. 8), is also in the second life period. The median disc is completely ossified and fused with the pelvic bones which are also united with each other. No trace exists of the lines of union and barely an indication of the line of fusion of the epiphysis on the ischial tuber.

The information gleaned from the Wombat skeletons is amplified by reference to those of the Macropodidae. First of these we take a specimen of Petrogale xanthopus B 192 (Fig. 6). This example is from early in the second life period as evidenced by the obviously recently united acetabular elements. The lower nodule is well ossified and so is the epiphysis for the tuber but between these is a strand of cartilage in which no ossification exists. The bony center for the upper nodule has quite recently appeared and in connection with it a flake-like ossification has occurred in the median disc, this being visible from behind in the narrow upper gap between the pelvic bones. There is as yet no fusion of the pelvic bones together.

Next in order of sequence is a specimen of Macropus bennetti B 182. This time there is no vestige of the lines of union of the acetabular elements but the animal was still in the second life period. The ossifications for the lower nodule and the epiphysis of the tuber approach but still leave an intervening area of unchanged cartilage. The upper nodule is completely ossified though not yet fused with the pubic bones. From it there projects downward a flat tongue of bone, the further development of the flake seen in the last specimen, to approach an upwardly directed tongue from the lower nodule also growing at the expense of the symphysial cartilage. Again there is no effort at fusion of the two pelvic bones.

An example of Dendrolagus inustus B 193 (Fig. 5) from the second life period affords opportunity to study the further development of the symphysial ossification. In this the lower nodule is in bony continuity with the epiphysis of the ischial tuber. From the nodule ossification extends upward and just meets the down growing ossification from the upper nodule. At the mid-vertical point of the long symphysis it is evident that the ossification tends to be somewhat central in the cartilage but higher up the bony development is much greater ventrally. Indeed in this location the bone spreads out laterally so that the upper nodule lies rather on the ventral surface of the pubic symphysis although from this nodule a keel projects backward between the pubic bone and it is the hinder margin of this keel which can be seen from the back on the last specimen. A dorsal margin has grown up to delimit the sym-

physial face of the pelvic bone and is continuous throughout. Hence the stage of development is a little more advanced than that of Phascolomys B 601.

The succeeding phase is illustrated by Macropus bennetti B 181 (Fig. 7) from the second life period. The two pelvic bones are united immediately beneath the upper nodule which itself is median in position and lies on the ventral aspect of the pubic bones but is not yet united to either. The union of the pelvic bones is equally marked on both back and front but does not transgress the lower limit of the pubis in a downward direction. Ventrally the ununited portions of the pubic bones above permit a glimpse of the median tongue of bone just below the upper nodule. No such appearance is noted between the approximated but ununited ischial rami forming the lower part of the symphysis.

Specimen B 191, Potorous tridactylus, is at the end of the second life period for the epiphyses of its long bones are almost completely united. In this skeleton the pubic bones are wholly fused dorsally and the ischia are fusing. Both upper and lower nodules are in process of union with the pelvis and a median crest has appeared, most strongly marked on the ventral aspect of the lower nodule but still of recognizable proportions vertically throughout the entire ventral symphysial line.

Bettongia lesueuiri, B 598, is in the third life period. In it there is complete fusion throughout the symphysis and the ventral crest is well marked especially on what was the lower nodule. No indication of the fusion lines of any part of the symphysis remains.

From the foregoing description it is clear that in the Diprotodonts complete ossification at the symphysis and fusion of the two pelvic halves occurs before the end of the second life period. This is what we suspected in the Monotremes although because of the condition of the vertebral centra in those aberrant animals we could not be quite sure. We note that the symphysial ossification takes the form of a somewhat dumb-bell shaped median bar lying mainly upon the ventral face of the symphysis but extending somewhat between the symphysial faces as a thin median disc. We see also that the bar with its expanded extremities is formed not by a single center of ossification but through the fusion of a succession of median bony centers along the symphysial and ventral margin of the ischio-pubic ramus, continuous morphologically with the ossification extending as an epiphysis from the ischial tuber. Of the several ossification centers indicated, that which ultimately forms the lower extremity (lower nodule) ossifies first. This is fol-

lowed by ossification in the upper extremity (upper nodule), and from each of these centers ossification extends in the substance of the median disc with or without the help of accessory ossification centers until complete ossification has taken place.

We turn then to the Polyprotodontia.

There is an example of Didelphys virginiana in the collection, B 177, in the second life period, showing ossification of upper and lower nodules slightly more advanced than the condition present in Petrogale B 192 above.

There is also a specimen of Thalacomys minor B 185, likewise from the second life period, which shows a condition intermediate between those of Dendrolagus B 193 and Macropus B 181 previously mentioned.

The general confirmation which the two foregoing Polyprotodonts give to the method and age relationship of symphysial ossification as described for the Diprotodontia is continued by other examples.

Among our Dasyuridae there is a specimen of Antechinomys laniger B 190 in the second life period, showing a stage immediately following that of Macropus B 181 for the pubic bones are in process of uniting in the upper part on the dorsal aspect. We have also a stage like that of Dendrolagus B 193 in a young Phascologale flavipes B 189 in the second life period.

There are two skeletons of Sarcophilus ursinus, both curiously enough of the same stage of the second life period for both have the epiphyses of the long bones in the same state of incomplete union. Their numbers are B 178 and B 238. The stage of symphysial ossification illustrated by these two is the same. It is just a little more advanced than that of Petrogale B 192 above and in conformity with this the lines of fusion of the three acetabular elements are visible only in a strong light.

A later stage is exemplified by Thylacinus cynocephalus B 194 for in this animal the epiphyses for the upper ends of the humeri and femora alone of the long bones are still ununited. The stage of the symphysis is somewhat earlier than that of Potorous B 191 for the pelvic bones are not completely fused above and below on their dorsal aspect although both nodules are uniting with the pelvis and the median vertical crest is forming.

Our other marsupial skeletons are too far advanced for the present study. Notoryctes typhlops B 134, it must be noted, has a pubic but no ischial symphysis. This animal is in the third life period. The pubic bones are completely fused and there is no remaining indication of the method of union. It is worth while noting that there is also no remnant of the fusion line for the epiphysis of the tuber.

Ossification at the marsupial symphysis may be summarized in the following manner. No matter what the Family, in Polyprotodonts and Diprotodonts alike, there is one type of metamorphosis and the various stages of this metamorphosis present a constant relationship to age. Practically the entire symphysial metamorphosis occurs during the second life period, that is to say the period of union of the epiphyses of the long bones. This period commences after the fusion of the three acetabular elements. The succeeding stages of metamorphosis are quite definite. In the cartilage of the pubic-ischial symphysis there appears a bony center for the lower nodule at the point of bifurcation. This is followed by the occurrence of a bony center for the upper nodule. From each of these centers a bony tongue extends through the vertical length of the symphysial cartilage, the mid-vertical point being the last to ossify. Ossification at the same time extends backward over the symphysial face of the pelvic bones but the bulk of the ossification, especially above, occurs ventrally. There are now definite upper and lower median nodules united by a long flake like bony disc. At the same time the horizontal ridges and furrows of the symphysial face become limited behind by the development of a dorsal margin to the symphysial face which is broader dorso-ventrally in its pubic part. The median disc now fuses with the two pelvic bones which thus become united. The union first takes place just below the upper nodule. It is then carried upwards and downwards on the dorsal aspect. Later the upper nodule fuses with the pubic bones. After this the lower nodule unites with the ischia and finally the median ventral crest appears.

It does not seem important at this stage to discuss the condition of the symphysial cartilage although there are many Dasyuridae in the Hamann Museum still in a recent state. These would doubtless give the successive stages for the Polyprotodontia much more completely than has been outlined above, but the material seems too valuable to use up for the illustration of a sequence already well established.

We have not so far made any comment upon the amount of participation of the ischium in the symphysis as regards Marsupials. Our specimen of Notoryctes B 134, in the third life period, is important in this respect. The very small obturator foramen may be taken as representing the junction between pubis and ischium. The symphysis is very short and judged by the indication just mentioned is entirely pubic.

Looking over the whole Marsupial series one is struck with the very slight extent to which the ischium actually does take part in the sym-

physis. Practically only the lower extremity is ever ischial, the rest of the surface being invariably pubic. As the description of the various orders progresses it will become obvious that this type of symphysis is the characteristic Marsupio-Placental form. From it there are variations which lead either to elimination of the ischial and shortening of the pubic portion, or to secondary increase of ischial participation. Both kinds of variation are to be found in some orders and they have no taxonomic value.

INSECTIVORA

One of the most important, indeed for our purpose probably the most central group of mammals is the suborder Menotyphla comprising the Oriental tree shrews and the African jumping shrews, the reason for thus emphasizing the difference in habit of the two families will shortly become clear. All the members of this suborder are difficult to obtain and we have to content ourselves as yet with two specimens of Tupaia, one still in the hide, to represent the whole suborder.

Tupaia tana B 211 (Fig. 9) is in the fourth life period, a very important stage in this investigation. The epiphysis for the ischial tuber is fused. The symphysis is long and though mostly formed by the pubic bones is completed at its lower extremity by the ischia. It is well to recognize however that the ischia play a relatively insignificant part in the formation of the symphysis. The two halves of the pelvis are not yet even beginning to fuse at the symphysis, at least behind. On the ventral aspect a long and somewhat moniliform rod of bone has developed in front of the line of the symphysis and is fusing with both sides. Above this rod expands slightly and sinks more deeply between the upper ends of the pubic bones. Below the same thing happens and this lower triangular expansion completes the symphysis caudally and is directly continuous on each side with the fused epiphysis for the tuber. The condition of the symphysis therefore which was found in the Marsupials occurs again in this animal. We have not so far begun to compare the successive stages of the mammalian symphysis in general with those of Man, but we shall see later that the stage just described corresponds with phase VI inasmuch as the ventral symphysial margin is developing by the formation of the median bar.

The entire pelvis of Tupaia is strikingly like that of the Lemurs and it is because of the close ancestral relation of this animal to the Lemurs that I emphasize its importance. In spite of its being arboreal the symphysis of Tupaia retains the primitive Marsupio-Placental character

(Gregory 11 p. 279). This relative length of the symphysis in Menotyphla is a marked distinction from the exceedingly short symphysis, if symphysis there be at all, in the Lipotyphla. Even in Ptilocercus, the other member of the family Tupaiidae, according to Gregory (12 p. 249) the symphysis is "very short." Again in Macroscelides the symphysis is short according to Gregory's statement in 1910 (11 p. 283) though the same author describes it as long in 1913 (12 p. 249). In the absence of further information one would infer that the symphysis in Macroscelides is shorter than in Tupaia and longer than in Ptilocercus. One may then ask the question whether Ptilocercus or Tupaia shows the more primitive symphysis. Later we shall find that both arboreal and terrestrial forms exhibit a tendency to variation of the the symphysial length. One might infer that the ancestral symphysis was short. The reptilian symphysis however includes the ischium to a marked extent and this condition is retained in the Monotremes. To this subject of the primitive mammalian symphysis we must return after the data are all presented but for the moment one may state the probability that both Tupaia and Macroscelides present fairly primitive and typical Marsupio-Placental symphyses. This means that the primitive Marsupio-Placental symphysis was relatively short and therefore unlike that of Monotremata in not engaging the ischia to any great extent.

Turning now to the Lipotyphla we find that the symphysis becomes exceedingly short or is even absent altogether. There is no doubt that this shortening is a secondary modification and evidence accumulates to show that there are differences in the length of the symphysis within a single species. The difference may have a certain relation to sex as in certain Rodentia (6) but it is an indication of a progressive specialization nevertheless. This is not the place for a full discussion of the problem but the reader may be referred to Gregory's notes on Solenodon by way of example.

"The pelvis of an adult female (Amer. Mus. No. 28271) differs markedly from one of the same species figured by Leche (1907, p. 82) in the ventral view: instead of the long symphysis pubis being present, the opposite ossa innominata are widely separated in the dried skeleton and the symphyseal region of the pubis ends in a point as in Erinaceus."

Our specimens of the Lipotyphla include one or more complete skeletons of the following: Ericulus, Echinops, Hemicentetes; Potamogale; Chrysochloris; Hylomys, Gymnura, Erinaceus; Talpa. All are so specialized that they are beyond the range of this discussion. At

most, as in the Erinaceidae and in Hemicentetes the symphysis consists of a fibrous band connecting the pointed cartilage covered symphysial tips of the ossa pubis.

DERMOPTERA

Our single specimen of unknown sex, Galeopithecus volans B 544, is in the fourth life period. It represents a very short symphysis which is cartilage covered, the cartilages of the two sides being quite separate from each other. There is no ossification in either cartilage and when the cartilage is stripped off, the specimen being preserved in fluid, there is merely a rounded bony surface of cancellous tissue quite unlike the typical mammalian symphysial face. There is no definite dorsal margin as one might expect at this stage, and certainly no suggestion of extremities or of ventral margin. It is indeed very like the condition in the Edentates soon to be presented and therefore well on the way to the condition shown in the Erinaceidae.

The markedly short symphysis is particularly interesting in view of Flower's statement that it is long and finally becomes fused (10) and again in reference to the possibility that the shortness may be a progressive specialization as suggested in the case of Solenodon above.

CHIROPTERA

Our Microchiroptera show a very specialized symphysis like that of the Erinaceidae. The progressive specialization in these animals shows a sexual difference. We have Rhinolophidae only as skulls. In these animals, which alone among microchiroptera possess a symphysis, the symphysis could give us no profitable information in the present connection. We have only skulls of the Megachiroptera.

RODENTIA

Reference has been made to Chapman's work on the Rodents (6) and it is therefore unnecessary to do more than remind the reader of the three groups into which Chapman divides the symphyses of this order (see p. 343). At the moment we are concerned with those members only which still possess a fairly generalized symphysis.

It is usually claimed that both pubis and ischium take part in formation of the typical mammalian symphysis. We have noted in Tupaia that the ischium plays a very small rôle in symphysis formation and this view is confirmed in the case of the Rodentia by a young specimen of Arctomys monax B 127 (Fig. 10) in the first life period. Its im-

portance lies in the fact that, as in the case of other Sciuromorphs, its symphysis is long. This great length of the symphysis is not due however to participation of the ischia in its formation. Reference to the figure shows at once that the symphysis is entirely pubic in composition. This fact should be borne in mind in the interpretation of other mammalian symphyses. It will be recalled in the section on Ungulata.

Our material referable to this order is not either very great or comprehensive, nevertheless the observations about to be recorded are extremely suggestive, when compared with the evidence culled from the Marsupials, of a difference existing between Marsupials and Rodents as representing a Placental order, in the age-relationship of pubic metamorphosis. It is well therefore to remind ourselves of the features presented by successive phases of human pubic metamorphosis. In former publications I have stated these as follows (e. g. 28 pp. 1-2).

Phase I. Typical ridge and furrow formation with no sign of margins and no ventral bevelling.

Phase II. Foreshadowing of ventral bevelling with slight indication of dorsal margin.

Phase III. Progressive obliteration of ridge and furrow system with increasing definition of dorsal margin and commencement of ventral rarefaction (bevelling).

Phase IV. Completion of definite dorsal margin, rapid increase of ventral rarefaction and commencing delimitation of lower extremity.

Phase V. Commencing formation of upper extremity with increasing definition of lower extremity and possibly sporadic attempts at formation of ventral rampart.

Phase VI. Development and practical completion of ventral rampart with increasing definition of extremities.

Phase VII. Changes in symphysial face and ventral aspect of pubis consequent upon diminishing activity, accompanied by bony outgrowths into pelvic attachments of tendons and ligaments.

Phase VIII. Smoothness and inactivity of symphysial face and ventral aspect of pubis. Oval outline and extremities clearly defined but no "rim" formation or lipping.

Phase IX. Development of "rim" on symphysial face with lipping of dorsal and ventral margins.

Phase X. Erosion of and erratic, possibly pathological osteophytic growth on symphysial face with breaking down of ventral margin.

It may be doubted how one can utilize for symphyses in which fusion of the two pelvic halves takes place the phases described for a type of symphysis in which there is permanent separation. As a matter of fact there is no great difficulty as far as phase VI. Fusion cannot occur before development of the ventral margin in one form or another. The evidence shows that in cases where fusion does occur it takes place at the stage covered by late phase VI and early phase VII. This will become clear as we proceed. It is mentioned now in order to avoid confusion. Pathological fusion on the other hand does not occur at a definite stage of metamorphosis; it may take place at any time in the life of the animal and indeed may probably be hastened by injury as in Lemur catta B 137 later to be described.

A specimen of Mus norvegicus albinus B 594 in the second life period shows a much shorter symphysis, entirely pubic, without a trace as yet of ossification of nodules, but there is quite plainly a differentiation between the articular cartilages of the two sides which meet in the symphysial plane.

Later in the second life period when only the epiphyses at the knee and shoulder remain ununited there is still no ossification of symphysial nodules. This is illustrated by Mus musculus B 287 and by other specimens which may be passed over. At this same stage however there is evidence of a growing dorsal margin very plainly seen in Mus decumanus B 292. One must admit then that relatively late in the second life period the Rodent symphysis has reached only phase III of its metamorphosis.

The delay in metamorphosis is not always so marked. A specimen of Hydromys chrysogaster B 294 in which the epiphyses of the long bones are ununited only at the shoulders and partly at the knees shows beautifully the formation of an upper bony nodule, median in position, in the cartilage of the symphysis. This lies entirely upon the ventral aspect of the symphysis. In the lower part there is a triangular nodule typical in appearance and also median in site, plainly the continuation of an epiphysial ossification along the ischial ramus from the ischial tuber. The two halves of the pelvis are not yet united. One must class this specimen in phase V of metamorphosis.

Carrying our research among the Hystricomorpha we find evidence that symphysial metamorphosis is delayed in the Myomorpha if the evidence just cited be representative of this section of the Rodents. The very aberrant and Edentate-like pubis of Coendou prehensilis may be omitted for although our specimen B 263 is in the second life period

and shows no ossification at all in the symphysial region, the form of the pubis itself suggests that whatever its metamorphosis may be it would be in no way representative of the Hystricomorphs.

Our specimens of Erithizon dorsatus are of the second life period but not far enough advanced to show ossification of the symphysial epiphyses. There is however one example of Trichys guentheri B 264 (Fig. 11), which is quite important on account of the age relationship of its pelvis. It is early in the second life period as evidenced by the lack of fusion of the epiphyses at the elbow and also by the plainly recent fusion of the acetabular elements. In spite of its youth the dorsal margin of the symphysial face is already completed and ossification has occurred throughout the epiphysis from the ischial tuber to the lower extremity of the symphysial area. There is no lower nodule or any suggestion that one may ultimately form. Instead the terminal portions of the epiphyses just mentioned appear to take its place. There is no upper nodule or median disc.

The last of the Simplicidentata of the second life period to be recorded is Dolichotis patachonica B 267 (Fig. 12). The upper epiphyses of humeri and tibiae alone remain ununited and the epiphysis of the ischial tuber and ramus is fully ossified and united with the ischium. Its ventral extremity however forms a nodule which, together with the fellow of the opposite side, represents the lower symphysial nodule the site of which they occupy. There is no upper nodule or ossified median disc. Nor is there any indication of a rampart or definitive margin forming at the ventral margin as might be anticipated in a bilaterally forming structure. Both this specimen and the last are in phase IV of pubic metamorphosis.

The Guinea-pig would be an interesting animal to investigate in this regard since Flower states that its symphysis remains ligamentous (10). We do not possess the necessary material for the purpose.

Passing now to the later life period of the Simplicidentata there is only one specimen which merits attention. This is Arctomys monax B 300 in the late fourth period. In this the pelvic bones are completely united at the symphysis and a median crest has formed. It is quite apparent still that no lower nodule has formed but that, instead, the ventral extremities of the ischial epiphyses have taken its place and terminated the symphysial face below. The lower quarter of the symphysis is ununited behind. No upper nodule has developed but the pubic bones by some slight growth have met and fused in the median line.

The information gleaned from the Duplicidenta confirms in a general manner that just cited from observations on the Simplicidentata.

One may therefore sum up the age relationship of the Rodents in the following manner. Early in the second life period pubic metamorphosis has reached no more than phase I. Relatively late in this period phases III and IV follow each other rather rapidly. Fusion of the pubic bones occurs late in the fourth life period at phase VII. The only exception to this general rule is shown by Trichys. There is considerable delay in pubic metamorphosis when compared with that of the Marsupials. A further and important distinction is the tendency to completion of the symphysial face by bilateral rather than median ossification.

EDENTATA.

In our Edentate material the stages are missing which would show the precise method of change at the symphysial region but we have specimens of Manis, Bradypus and Tamandua in the second life period with the symphysial cartilage still uninvaded by ossification. There is one example of Choloepus didactylus from Costa Rica (B 275) in the third period with the pubic bones entirely fused so that no trace of the lines of fusion remains. Since the third period in the Mammalia is relatively short it is apparent that in the Edentates pubic metamorphosis passes through all phases rapidly. Though its inception is delayed when compared with the Marsupials it is completed somewhat earlier. This is what might be expected from the short and aberrant type of symphysis.

As for the precise type of metamorphosis we have no certain information in the material here but there is a specimen of Dasypus sexcinctus (B 276) in the fourth life period showing a suggestion of a median lower nodule in the already long fused symphysis. This lower nodule builds about half the height of the bony symphysis. It is most instructive to compare it with Albrecht's Fig. 1. (1). In Albrecht's case the entire symphysial area was formed by an "interpubic bone" which appears to be the homologue of this lower nodule. Concerning the homology however there is not yet definite proof. Albrecht's Figs. 2, 3, 4 are very valuable in a study of the Edentate symphysial region. From them and the text in conjunction with our material one gathers that the area is quite variously built up in this aberrant order. There may be an interpubic bone narrow antero-posteriorly but elongated transversely; or the bone may be a much smaller ossification and, as in B 276, it may not build the entire symphysis. In later life fusion takes place so completely that there is no separately distinguishable

interpubic bone at all. Albrecht's Fig. 4 shows a young Manis somewhat older than our young specimen. The symphysial area in this animal possesses two centers of ossification from which combined the interpubic bone is formed. This retention of the original bilateral ossification is extremely interesting in so specialized a symphysis.

The value of the Edentates in this study is only appreciated after other orders of Monodelphia have been considered. Pubic metamorphosis is comparatively late and this is probably a very significant fact. But in consequence also of the retrogressive nature of their symphysial area metamorphosis is rapidly completed when once begun and even the appearances of the successive phases in metamorphosis and of the bony surfaces themselves are considerably modified and retrogressive. In this respect comparisons may be made with Galeopithecus and with Erinaceidae especially Gymnura.

UNGULATA

In the remaining mammalian orders which we shall discuss there is a clear symphysial distinction. In the Ungulates the true symphysial face is not simply pubic in nature but is confined to the body of the pubis. The so-called ischial participation is an approximation of bony ridges rather than an articulation. In the Primates and Carnivores on the contrary there is a distinct tendency to enlist more of the pubis or even the ischium in the symphysis. We shall therefore take the Ungulates under consideration first. In these animals there is a distinct sexual relation in the shape of the symphysial face which will be mentioned in the course of description.

Commencing with the Artiodactyla we shall utilize the Deer first because our series of these animals during the second, third and fourth life periods is complete. These periods are found to be the most important for our present study.

In the preceding pages no attempt has been made to distinguish any sex difference in the age relationship of pubic metamorphosis. In many specimens the sex is uncertain but in those in which it is definitely known sex plays no important rôle in this matter. All our American deer were given to us by the Municipal Authorities under the administration Mr. Newton D. Baker. In these as in all our other Ungulates the sex is known: it will therefore be worth while to state the sex and thus show that in these animals there is no definite sex linkage in pubic metamorphosis.

The first specimen is a male Odocoileus virginianus B 639 from very late in the first life period, so late indeed that there is only a small portion of the suture between ilium and ischium still remaining unfused. The third permanent molars are erupting. The symphysial face is entirely pubic and involves the body of the pubis alone. The inferior ramus is very slender and shows no continuation of the articular surface. The ramus of the ischium which fuses with this pubic ramus likewise exhibits no articular area. The oval articular face of the pubis is broad antero-posteriorly, this being a characteristic of the male. Its dorsal margin is almost completed and the honeycombed surface adjacent is already distinctly smoother than that nearer the center of the area. The upper and lower extremities are well defined without the aid of any epiphysial nodules, but the ventral margin is as yet unformed and instead of a honeycombed surface the pubis shows horizontal ridges and furrows adjacent to it. The appearance of the dorsal margin in spite of the other features of the symphysial face which may result from specialization indicates that we must classify the specimen as belonging to phase III-IV of pubic metamorphosis.

Whatever doubt there may be as to the precise classification of the foregoing pelvis there can be no uncertainty regarding the two succeeding ones. These are Odocoileus virginianus B 649 (Fig. 14) and B 642. Both are from the second life period and possess fully erupted third molars. The symphysial face of the former is somewhat broader than that of the latter but apart from this one description holds for both. The dorsal margin is fully formed and a narrow dorsal platform adjoins it. The extremities are well defined but there is no attempt at formation of a ventral margin of distinct outline like the dorsal. The ventral part of the symphysial face is slightly bevelled and down it run fairly typical horizontal ridges and furrows. Both examples are clearly in phase V of pubic metamorphosis.

The next specimen from very late in the second life period, the third molars long erupted, is a young Wapiti, Cervus canadensis B 196. There is no difference in the symphysial face of this specimen from those of the last two except that, being much larger, its features are more striking. That the animal was a little older is indicated by the commencing fusion of the ischial epiphysis.

Odocoileus virginianus B 648 is a female animal at the extreme end of the second life period. Apparently the ischial epiphysis does not fuse so early as in the Wapiti; at least in this and in the next it has not fused. The symphysial face is narrow from before backwards, this being

typical of females. Except for the ventral part the symphysial features are those of the foregoing. But now we see the ventral portion becoming distinctly bevelled and its texture changing to a finely granular condition. This is undoubtedly the precursor of formation of the ventral margin. It is probable that one should classify this specimen as on the border-line between phases V and VI.

The next example, namely Odocoileus virginianus B 634 (Fig. 13), illustrates the immediately succeeding stage. The animal is a female of the third life period whose third molars are erupted and much worn. The symphysial face has the usual honeycombed appearance but the ridges are taking on a waxy surface which we have learned to associate with inactivity in whatever skeleton or location it is found. The lower half of the ventral margin is clearly defined by a ridge growing up in association with ossification of what corresponds to the median disc in the Marsupial. There is no attempt at fusion. When the two pelvic bones are articulated together only the pubic bodies and the lower ends of the inferior ischial rami come into contact. Between the inferior rami of the pubes and between the major portions of the ischial rami there is a long narrow fusiform hiatus. There is no indication of the lower nodule which is described in the following pelvis.

The key to these appearances is given by Odocoileus virginianus B 633 (Fig. 16). The specimen is a female late in the third life period. Already some fusion has taken place between the two halves of the pelvis. The fusion is not yet direct except between the lower ends of the inferior ischial rami which are united by interlocking teeth to form a suture-like line. No indication of these "teeth" was visible on the last specimen. Throughout the median vertical line of future union of the two pelvic bones there is a narrow pencil of newly formed bone, not passing backward but lying on the ventral aspect alone. It extends upward to a point halfway along the ventral edge of the syn-symphysial face and downwards to the area of fusion of the ischial rami which it covers in front by expanding into a triangular nodule continuous on each side with the extension of the epiphysis of the tuber. The lower nodule just described is already completely fused with the ischia. The median pencil or disc is fused almost throughout with the left side of the pelvis but on the right it is united at its extremities only. When previous writers (e. g. Flower 10) have spoken of the synphysis of Ungulates involving both pubis and ischium they have not made clear the important part played by the median pencil or disc and they have not noted that the ischial involvement is more or less supernumerary.

That the ischia readily separate will be obvious before this description of the Ungulate symphysis is concluded. Another important point which deserves emphasis is that fusion between the two sides of the pelvis is occurring directly in the case of the ischial rami, indirectly in the true or pubic symphysial region through the activity of the median disc, at this stage which must be identified as phase VII of pubic metamorphosis.

It is this median pencil of bone, so often lost in maceration as it was in the maceration of our younger specimens, which corresponds to the real ventral margin. This median ossification occurs probably rather early in the second life period and remains separate from the pelvis itself for a considerable time after its appearance. At its lower extremity it bifurcates, one limb extending along the ischial ramus of each side. Judged simply by the unusually early appearance of this median ossification the Deer would have to be represented on the graph (Fig. 45) very close to the Marsupials. And such a position would be borne out by many of the features of the symphysial face. Nevertheless just as we found in human exceptions that certain characters are more stable than others, so now it would seem that the extent to which the dorsal margin has developed and ventral bevelling has occurred are more trustworthy features than the precise stage at which the first ossification for the median bar is found or the very specialized face acquires delimitation of its extremities.

Odocoileus virginianus B 78 a male at the extreme end of the third life period, shows the complete fusion in front at the symphysis. The upper end of the median disc is, as it were, plastered over the as yet ununited ventral margins of the symphysial faces. Throughout its length the disc is raised to form a crest and, as in the Marsupials, the crest projects in distinct promontory form from the lower nodule. Although the median disc does not extend backwards it is visible from behind in the long narrow fusiform hiatus extending from the pubic bodies above to the site of ischial fusion below and here it is the sole medium of union between the two halves of the pelvis Unlike the preceding specimen the lower nodule actually unites the ischia in this animal and the lines of its fusion with these bones can still be traced. The only site where the pelvic bones are directly united is at the lower half of the true symphysis which, as we have seen, is formed by the bodies of the pubic bones only. In deciding upon the stage of pubic metamorphosis attained by this specimen we must take into account the incomplete ventral margin in its upper quarter and the absence of any

union of the symphysial faces themselves. It will be recalled that only the lower halves of the dorsal margins are fused. The pelvis must therefore be assigned to the end of the sixth phase of pubic metamorphosis or the beginning of the seventh.

The Old-World deer must carry us on through the succeeding stage. The first is a male Muntiacus muntjak vaginalis B 607 (Fig. 15) in the fourth life period. Here the union is very slightly further advanced than in the last. The lower nodule is distinctly seen from behind and except for the absence of a median crest there is no difference in this symphysial area from that of the last. It is definitely in phase VII.

Hydropotes inermis B 606 also a male in the fourth life period, shows complete fusion both in front and behind throughout the symphysial area and is the sort of specimen which on superficial examination would lead one to suppose that pubis and ischium take equal part in the symphysis. This must be assigned to phase VII+ since we have no way of defining it more accurately at the moment.

The last part to fuse completely in spite of its getting a relatively early start is the pseudo-symphysis formed by the rami of pubis and ischium. This is shown by a specimen of cervus canadensis B 195 in the latter part of the fourth life period. This specimen is only slightly less advanced than the foregoing but fusion behind comprises only the true symphysis and the lower nodule whereas in front complete fusion has taken place.

We pass now to other sections of the suborder Artiodactyla and find that they confirm the observations made upon the larger material of the Cervidae. Hence a very short description will suffice.

B 469 Dorcatherium aquaticum aquaticum, a female of the second life period, shows a well developed margin of the symphysial face and a dorsal platform extending over nearly one half the surface. The bevelling of the ventral margin previous to the formation of the median crest has not yet begun. The lower extremity is still indefinite. One must assign the pubis therefore to phase III.

Tragulus javanicus borneanus B 467, also a female but in the fourth life period shows complete fusion of the two halves of the pelvis both pubes and ischia, back and front, except at the extreme upper extremity. The median crest is forming. The specimen is therefore in phase VII.

Leaving the Chevrotains we pass to the Bovidae in the collection. There is a specimen of Bos taurus in the first life period (B 643) but this is a dwarf which died at two years of age measuring only forty inches in height to the withers. The symphysial metamorphosis has been

quite precocious; the dorsal margin and platform are well developed, the ventral bevelling is present and the surface in general exhibits that waxy appearance associated with stagnation of metamorphosis. The specimen is an anomalous example of phase III and should therefore receive no further consideration at present.

Two Angora goats, Capra hircus, are quite important. One of these, a young male B 641, is in the second life period. The dorsal margin of the symphysial face is just beginning to develop and massive ridges and furrows without a trace of ventral bevelling are still well shown. There is no indication of the lower extremity. The specimen is therefore at phase II. The other goat B 640 is a female at the extreme end of the third life period. There is complete fusion of the ischial epiphyses. The lower median nodule is likewise completely fused and the median disc has united the two ischial rami in front. The two pubic bones are slightly united in front only. One cannot place the specimen as more advanced than phase VI.

The last Artiodactyl to receive attention is a young male Tetraceros quadricornis B 603. This is in the second life period and shows a well formed dorsal margin and a dorsal platform extending over one third of the symphysial face. There is no ventral bevelling and no sign of the lower extremity. On the contrary the horizontal ridges and furrows are very clear. The symphysis is therefore in phase III.

In all the foregoing Artiodactyls the sex character of the pubis is perfectly distinct. In the male the symphysial face is biconvex and deep antero-posteriorly: in the female it may be concavo-convex and is always narrow from before backwards.

PERISSODACTYLA

Our collection of Perissodactyl pelves is very meager but there are a few specimens which are of significance in that they confirm the typical Ungulate symphysis.

A young male Tapirus indicus B 262, from the second life period, has its first permanent molars erupted and shows a symphysial face with typical Ungulate rugosity, no ventral bevelling and only the merest indication of formation of the dorsal margin. One cannot classify it beyond phase II which is probably its correct position. The ossifying epiphyses for the ischial tubera have not yet united with the main mass nor is there any attempt at fusion of the two halves of the pelvis.

Among the Equidae we have three examples, all of rather advanced stages. The first is a male Equus burchelli B 242, estimated from the

condition of the teeth as about twenty years or somewhat older. It is a menagerie specimen from the borderline between the fourth and fifth life periods. The pubis is biconvex on antero-posterior section, the typical condition in the male Ungulate. The two halves of the pelvis are completely fused, and in this fusion the ischia take part although, unlike the pubic bones, they present no directly articulating surface. There is no sign of roughness or irregularity on either front or back of the line of fusion.

That the ischia are the last to use is illustrated by a mare of Equus caballus B 534 of the fourth life period. This animal is a little younger than the Zebra just described: it has a pubic symphysis convex in front and concave behind. Distinct dorsal concavity is much more characteristic of the female Perissodactyl than of the Artiodactyl. Fusion in this case extends throughout the symphysial area except in the dorsal surface of the part formed by the ischia.

Fusion of the ischia however may remain incomplete. This is shown by another mare of Equus caballus B 533, an animal in the late fifth life period. In spite of long standing fusion and considerable lipping of the joints the union of the ischia is incomplete in places. This is as one would expect since the relation of the ischia to the symphysis in the Ungulates is largely supernumerary.

Our only Hydracoid pelvis is from a specimen of Procavia brucei (B 241) of the second life period with the third permanent molars erupted. In this case the dorsal margin is forming but there is merely the first beginning of ventral erosion. The pubic symphysial face is therefore at phase III.

It is to be presumed that there is a ventral ossification in the Perissodactyls similar to the median bar described for Artiodactyls but if so it is very small and when united with the rest of the pelvis is indistinguishable.

CARNIVORA

In the Carnivora we meet with a fairly generalized Marsupio-Placental type of symphysis very different indeed from the aberrant Ungulate form. The ischium takes part in the lowest portion of the symphysis but for the most part, whether it is long or short, the symphysis is formed by the pubis.

CANIDAE

Apart from specimens too young for our purpose the Dogs at present in this osteological collection are from the fourth and succeeding life pe-

riods. As we have already seen the fourth period is one of great importance for the study of pubic metamorphosis.

Canis familiaris B 96 (Fig. 20) is a male pure bred Boston Bull thirteen months old and early in the fourth life period. The symphysis is a true one throughout; there is no secondary symphysis formed. The ischium participates with the pubis and thus an elongated symphysis is formed. The dorsal margin is completed and a dorsal platform extends over the entire surface except the ventral margin which is bevelled. Neither extremity is yet delimited although the dorsal margin in its completeness gives the impression at first that both are outlined in part. The ischial tuber has its epiphysis fused and extending forwards as isolated bony nodules to the region of the future lower extremity. One would assign the specimen to phase III.

Canis familiaris B 110 (Fig. 22) is also a male Boston Bull. It is two years old but is still in the fourth life period. The symphysial face now shows delimitation of both extremities and indeed the two halves of the pelvis are united by the triangular lower nodule which delimits the lower extremity. Ventral bevelling is apparent. Hence we may consider the specimen in phase V.

One might incline to suspect that the peculiar formation and development of the skeleton in the Boston Bull might have some influence upon age relationship. So far as pubic metamorphosis is concerned this is not the case for a mongrel dog B 309 and a Collie B 224 (Fig. 24), the skeletons of which are in the same general condition as that of B 110, show exactly the same features in the pubis. These also are in phase V.

A male Mastiff B 111 (Fig. 21), from the fourth life period shows the development of the ventral margin by simple ossification without the appearance of either rampart or bar. Both front and back of the symphysis are fused except for a small area at the back of the pubis. This specimen is in phase VI.

A male Collie B 128 (Fig. 23) illustrates the further stage. It is as usual from the fourth life period but ossification of the ventral margin is completed and the pelvic halves are entirely united. One must assign the pubis therefore to phase VII or possibly somewhat later.

B 403 (Fig. 25) which is a pure bred St. Bernard of uncertain age but undoubtedly senile and therefore in the sixth life period, shows beautifully the secondary changes of phase X occurring as an erosion of the ventral aspect. The specimen should be compared with B 111 (Fig. 21) in order to appreciate fully the difference between the building up and the breaking down of the ventral margin.

PROCYONIDAE

All these examples show a typical carnivore symphysis into which the ischium enters slightly.

Aelurus fulgens B 254, is early in the fourth life period. Fusion of the two pelvic halves has not yet commenced but it is clear that both upper and lower extremities are formed and that very soon fusion would have begun. One may therefore conclude that the specimen belongs to phase V. The ischial epiphysis is long united.

Cerecoleptes (Potos) caudivolvulus B 255, is also early in the fourth life period. Again the ischial epiphysis is completely fused but here it is obvious that the lower extremity of the symphysial face is formed by an extension of the ischial epiphysis. The specimen shows the bilateral nature of this admirably. The symphysis is in the same state as that of Aelurus, namely the upper and lower extremities are formed but there is no completion of the ventral margin or attempt at fusion. It is in phase V.

Bassaris astuta B 256, is in the fourth life period. The symphysis is much as in the two previous. There is fusion however at the upper extremity. One would place this specimen at the very beginning of phase VI.

Nasua narica B 253, is in the fourth life period. The symphysis is fused entirely except at the upper pubic part behind. It is therefore in phase VII.

URSIDAE

Owing to the relatively great death rate of bears in captivity during the second life period our macerated stock does not give a fair representation of the animals in the successive phases of pubic metamorphosis. Nevertheless there are certain points of general interest and importance which can be learned from this material.

Ursus americanus B 54, is a very young animal in the first life period after the union of the pubic and ischial rami. There is some fusion between the pubic and ischial components of the acetabulum but none between the ischial and iliac. The horizontal ridge and furrow system so well marked in older examples is not yet apparent but the general shape of the symphysial face already clearly indicates what it is to be in the adult animal. A noteworthy feature is the great length of the *pubic* symphysis. The specimen is assigned to phase I or earlier.

There are three specimens of Ursus americanus (B 635, male; B 636, female; and B 644, male) and one of Ursus malayanus (B 619), all

from the second life period after union of the epiphyses at the elbows. In each of these the dorsal margin is at an early period of its development; there is no dorsal platform or ventral bevelling. No indication of the delimination of either extremity is to be seen. Ossification has taken place in the epiphysis for the tuber and extends forwards for a short distance along the inferior ischial ramus. It is quite clear from these specimens that the extension of this epiphysis forms the lower symphysial extremity later on.

Ursus americanus B 129 is a female early in the fifth period of life. There is complete fusion of the two halves of the pelvis at the symphysis and also at the sacro-iliac joints. The epiphysis of the tuber can still be traced into the well developed lower nodule through a thinner connecting portion. No upper nodule has formed and no ventral rampart or bar completed the ventral ossification.

No sex distinctions of the symphysial face are discernible in the Bears.

MUSTELIDAE

Grison vittata B 646, is about half-way through the second life period. The tuber epiphysis is ossified but not yet fused; ossification does not extend beyond the tuber itself. As regards the symphysis, both extremities are still unformed and there is no ventral margin. The dorsal margin, however, is well developed. The specimen is therefore in phase III.

Galictis barbara B 616, is at the same stage of the second life period as Grison. Its symphysis is also in phase III.

Ictonyx lybica B 615, is in the fourth life period. Fusion has commenced behind in the symphysis, but the ventral margin is still in process of formation. The specimen is therefore in phase VI.

Mustela martes B 614, also in the fourth life period, likewise has its symphysis in phase VI for it is precisely similar in condition to that of Ictonyx.

FELIDAE

In the Felidae there is no sex distinction in form at the pubic symphysis. The symphysial face is long and extends to a certain degree on to the ischial ramus, somewhat more indeed as age increases.

At the extreme end of the first life period, that is to say when there is only a trace of the suture line between the acetabular elements left, are two skeletons, namely of Felis leo, B 72 and Felis domesticus B 64. Both show the same stage of pubic metamorphosis. The dorsal margin

is forming and adjacent to it is a narrow dorsal platform. No indication of either extremity has yet appeared. The apparent ventral bevelling is really the remnant of the ridge and furrow system. Both belong to phase III.

Felis leo B 334 (Fig. 18) is in precisely the same condition as the two previous examples. It is in the early second life period. We therefore assign it to phase III. The epiphysis for the tuber is ossified but the ossification does not yet extend along the inferior ischial ramus.

Felis domesticus B 63 is at the extreme end of the second life period. The dorsal platform has covered almost the whole symphysial face and the inferior extremity is becoming delimited. The specimen belongs therefore to phase IV. The tuber epiphysis is now fused to the ischium but the ossification still falls far short of the lower symphysial extremity.

Felis tigris B 611 (Fig. 17), is in the early fourth life period. The two halves of the pelvis are almost completely united, the dorsal ischial part lagging somewhat behind the dorsal pubic portion. The ventral margin is completed though the uppermost part has fragmented in the cleaning and the extreme upper limit seems not to unite, at least from the evidence of the next specimen. One would assign this pubis to phase VII.

Felis leo B 173 (Fig. 19), is in the fifth period. The symphysis is entirely united and seemingly quiescent except for the upper ventral pubic portion along the patent margin of which can be seen a well formed "rim" and the surface of which looks somewhat eroded. One must place this specimen in phase IX or possibly at the beginning of phase X. It should be contrasted carefully with B 611.

VIVERRIDAE

Herpestes punctissimus B 612, like other Carnivores shows clearly the bilateral nature of the symphysial cartilages. The epiphysis for the tuber is ossified and beginning to unite with the ischium. The bony process does not proceed far along the inferior ischial ramus. The dorsal symphysial margin is forming but probably there is not yet any attempt at formation of either extremity. It appears that this specimen is in phase III of pubic metamorphosis. The animal itself is in the second life period.

Cryptoprocta ferox B 244, is at the extreme end of the second life period. The tuber epiphysis is ossified and fused but does not extend more than half-way along the inferior ischial ramus. However the inferior symphysial extremity is becoming defined without the aid of an epiphy-

sis and ossification is appearing in the cartilage at the summit of the subpubic arch to form a lower nodule apparently median in position. No corresponding ossification can be seen in the cartilage of the upper extremity and no attempt is being made to form the ventral margin. The specimen is therefore in phase IV. It is doubtful how far the ischium participates in the symphysis of either this or the foregoing; it certainly takes only a meager part at most while in the next specimen it takes no part at all.

Suricata zenick B 613, is in the third life period. It has a very short symphysis into which merely the bodies of the pubic bones enter. One might expect that its unusual dimensions would have some influence upon its metamorphosis but this does not appear to be the case. In addition to the features shown by the last, this specimen exhibits clearly the delimitation of the upper extremity but not yet of the ventral margin. One assigns it therefore to phase V.

Viverra malaccensis B 243, is in the fourth life period. It possesses a typical carnivore symphysis of which the pubic portion shows commencing fusion behind. There is no fusion of the ischial part at all or of the pubic portion in front. The specimen plainly belongs to phase VI.

Arctictis binturong B 245, is in the fifth life period. The two halves of the symphysis which involves pubis only, are completely and long fused. The symphysis is therefore at least in phase VII.

PINNIPEDIA

The Pinnipedia are of no value in this study for their symphysis is very retrogressive. As in Zalophus californianus B 637, there is no distinct symphysial face.

PRIMATES

Interesting as are the symphyses of other mammals and important as we shall find them in the elucidation of the principles of pubic metamorphosis, the Primate symphysis far outstrips them in significance for the interpretation of the human form. In order then to secure a foundation for the better evaluation of the conditions found among the Primates we turn to the earliest Primate known, namely Notharctus of the Eocene. Unfortunately the symphysial area is not yet known in this animal but from Gregory's important and detailed monograph we gather the following significant information.

"The whole configuration of the pelvis of Notharctus indicates that the animal was an arboreal quadruped which did not sit fully upright but leaped about on all fours among the branches. . . .

"The pubis of Notharctus is not preserved, but from the close similarity of both the ilium and the ischium to those of lemurs, it is quite likely that the pubis was less extended antero-posteriorly than it is in Cebus." (13 p. 86)

"With regard to the postcranial skeleton the writer has made a very large number of comparisons between the vertebrae, limb and foot bones of modern Indrisinae with the homologous parts in the Eocene Notharctinae, with the invariable result that the conditions in the Notharctinae seemed to be evidently more primitive, potentially ancestral to the specialized conditions observed in the Indrisidae." (13 p. 216)

Now on our specimens of Cebus the symphysial face covers the pubic body and extends only slightly on to the pubic ramus. It is not so extensive as in Ateleus and other New World Monkeys. The area occupied by the symphysial face in Cebus is very much the same as in our Lemurs except that in some of them it is limited to the pubic body. The only pelvis of the Indrisinae which we possess as yet is that of Indris, but this is a more specialized animal than Propithecus. Our Indris has a symphysial face which covers both the body and ramus of the pubis and even doubtfully extends on to the ischium. This elongation may well be related to the different posture and loss of the tail. At any rate comparison of Milne Edwards' figure of Propithecus verreauxii with our Indris indris shows that the symphysis is much shorter in the former. We may take it then that the symphysis of the ancestral Primate was short, probably confined to the body of the pubis or but slightly extending on to the pubic ramus, and that its original limitations are fairly well preserved in modern Lemurs. With this background we may proceed to the consideration of the symphysis of modern Primates.

In the nomenclature of the Primates we shall endeavor to avoid confusion by adhering strictly to the nomenclature adopted by D. G. Elliott in his monograph upon this order (9).

LEMUROIDEA

In the consideration of Lemuroidea it will be of advantage in this work to take first the Galaginae, Lorisinae and Tarsiidae for in our examples of these the symphysis does not more than cover the pubic body whereas in the other members of the suborder it tends to extend on to the pubic ramus also.

Our Microcebus murinus Miller B 434 (Fig. 26) is a male in the second life period and by no means near the later part of that for the epiphyses around the knee joint are not yet united. In spite of this the tuberous epiphysis is completely fused. The dorsal symphysial margin is completely formed and the horizontal ridges and furrows are entirely obliterated by the dorsal platform. Upper and lower nodules are present and large but no rampart has yet appeared upon the ventral bevelled area. One must assign this animal to very late in phase V of pubic metamorphosis. Why it should differ so strikingly in age relationship from the other Lemurs I have no suggestion to offer at present.

In this animal, as already indicated, the symphysial face extends over the pubic body only. It is a very important specimen and probably indicates fairly closely the manner of pubic metamorphosis in the typical Primate. It is probably a more primitive form of pubic metamorphosis than any other specimen so far presented in this memoir.

Nycticebus borneanus Lyon B 136, a male at the extreme end of the second life period, shows an epiphysis for the ischial tuber in process of uniting. This epiphysis is ossifying as a narrow needle of bone along the subpubic arch but the ossification has not yet reached the pubic ramus itself and is therefore still far from the very short symphysial area. The dorsal symphysial margin is forming but there is no indication of either extremity and the ventral region shows only bevelling. The specimen is therefore in phase III. The symphysial face is limited to the pubic body and indeed does not cover all of that; it reminds one rather strongly of the Edentate symphysis.

Our single example of Tarsius borneanus Elliott B 135 is from the fourth life period. The dorsal margin of the symphysial face is well formed but there is no sign of commencing fusion of the two sides together. The ischial epiphysis is already considerably ossified but not yet united to the tuber. As an attenuated ridge fused with the main bone it extends along the subpubic arch and its continuity with the well ossified lower nodule is clearly discernible. The lower nodule is quite separate from its fellow of the other side and completes the lower extremity of the symphysial face. The upper nodule is also well ossified though, like the lower, it is not yet united to the pubis. It forms the upper extremity of the symphysial face. Ventral bevelling is plainly visible through the translucent cartilage but no indication of the ventral margin or rampart can be seen. The specimen is therefore in phase V. of pubic metamorphosis. Note that Tarsius has a short symphysis limited to the pubic body only.

LEMURINAE

Among the Lemurinae there are several examples. Lemur sp. B 138 (Fig. 28), is from the extreme end of the second life period. Again the symphysis is limited to the pubic body. There is commencing formation of the dorsal margin but no sign of the dorsal platform; the horizontal ridges and furrows remain unchanged. Neither extremity has begun to develop although the continuity between the lower nodule which has yet to ossify and the epiphysis for the ischial tuber can easily be made out along the subpubic margin which is still cartilage covered. Ventral bevelling has not begun. Symphysial metamorphosis has only reached phase II.

Lemur catta Linnaeus B 197, is a female in the fourth life period. The dorsal margin of the symphysial face is completely formed but the lower extremity is just commencing to define itself in spite of the long completed union of the tuber epiphysis. There is no indication of the upper nodule or extremity and from the ventral bevelled area no rampart is arising. The symphysis is therefore in phase IV. It extends over the pubic body and slightly on to the pubic ramus.

Lemur variegatus Kerr B 344 (Fig. 29), is a female in the fourth life period. The dorsal symphysial margin is completely formed. There is no union between the two sides of the pelvis. The new bone which has recently developed to build up the upper and lower extremities and the ventral margin is clearly distinguishable but the last mentioned is not completely formed. The epiphysis of the ischial tuber is long united. One must place this specimen in phase VI of pubic metamorphosis. The symphysial face extends over a small part of the pubic ramus in addition to the body.

Lepidolemur ruficaudatus Grandidier B 345, is a male in the fourth life period. Ossification and union are not yet complete in the epiphysis along the subpubic margin. The dorsal symphysial margin is complete; the lower extremity is forming and bony nodules appear along the line of the future ventral margin although these have not yet fused with the main bone. No sign of the upper extremity has appeared. Nevertheless the specimen is in phase VI of metamorphosis. The symphysial face scarcely encroaches on the pubic ramus.

Lemur catta Linnaeus B 137 is a male in the fourth life period which in earlier life suffered a fracture of the pelvis with good union but deformity. The pubic symphysis has been somewhat forced apart and fusion between the two sides has taken place but is anomalous in

its type. One must place it in phase VII. It is doubtful if this symphysial face extends on to the pubic ramus.

The foregoing specimens from the Lemurinae show that the greater part of the symphysial change occurs during the fourth life period. At the end of the second period symphysial metamorphosis is still in phase II; at the beginning of the fourth life period it is no further than phase IV but during this period all phases are passed through up to and including fusion which we have found commencing in other mammals late in phase VI. In the Lemurs it is pretty clear that fusion does not take place until phase VII. Reference to the graph of age relationships in pubic metamorphosis (Fig. 45) indicates that already in the Lemurs we see the same characteristically Primate age relationship which is found in Man.

In confirmation of the general statement of age relationship rendered possible by examination of the Lemurinae the following observations are recorded.

Indris indris Gmelin B 343, is a male from the fourth life period. The tuberous epiphysis is long united. The dorsal symphysial margin is formed and the dorsal platform has obliterated all indication of the original ridges and furrows. There is pronounced ventral bevelling but no suggestion of a rampart. The upper extremity is not yet defined and the lower extremity is barely indicated. The specimen is therefore at the very beginning of phase IV. It is further noteworthy that in this animal the symphysis extends secondarily downwards to include part of the ischium and that the lower extremity is forming without the intervention of a nodular ossification. This is possibly related to difference in posture and loss of the tail. The symphysial face in Propithecus does not extend so far.

Our example of Daubentonia madagascariensis Gmelin B 198, is a male in the fourth life period and shows a fairly typical lemuroid pelvis in all respects. The symphysis is rather long as would be expected from the sex but though it involves the pubic ramus it does not encroach upon the ischium. The tuberous epiphysis is long united and the dorsal symphysial margin is well formed. The lower extremity is formed by a sharply outstanding continuation of the tuberous epiphysis. There is no sign of a special upper nodule but there are indications that the ventral margin is about to commence upon the ventral bevelled face. The specimen should therefore be allotted to phase V.

ANTHROPOIDEA

In the Platyrrhine group we have no pelves of the Hapalidae. The following observations therefore apply only to the Cebidae.

CEBIDAE

Ateleus belzebuth E. Geoffroy B 141, is in the early part of the second life period. It is probably a young male. The tuberous epiphysis is not yet ossified but the extension of the cartilage along the subpubic arch into the symphysis is very plain. The symphysial face itself still shows the typical horizontal ridges and furrows of the adolescent stage and even the dorsal margin is scarcely attempted. There is no ventral bevel. We assign the specimen to phase II of pubic metamorphosis. The symphysial face involves pubic body and ramus but probably does not extend on to the ischium.

Cebus unicolor Spix, B 142, is also in the earlier part of the second life period but is slightly older than the last and the tuberous epiphysis is ossified over the tuber itself. The ossification does not extend along the subpubic arch. It is probably a female. The dorsal symphysial margin is well formed but there is no ventral bevel or any indication of either extremity. The specimen belongs therefore to phase III. Its symphysial face involves the pubic body and extends slightly on to the pubic ramus.

Aotus gularis Dollman (Nyctipithecus trivirgatus), B 342, is again somewhat older than the Cebus and is estimated to be in about the middle of the second life period. It is a female showing ossification of the tuberous epiphysis, the ossification extending along the subpubic arch almost to the lower symphysial extremity. The dorsal symphysial margin is well formed but the upper and lower extremities and the ventral margin have not yet defined themselves although there is considerable recent addition of bony tissue in the neighborhood of the upper extremity as in the last specimen. We still assign this animal then to phase III. The symphysial face is long; it involves pubic body and ramus, possibly extending slightly on to the ischium.

Alouatta palliata Gray, B 340, is stated to be a male although the pelvic features distinctly indicate female. It is in the very beginning of the third life period. The tuberous epiphysis is entirely ossified and partly united over the tuber itself. Along the subpubic arch the ossification extends as far as the lower symphysial extremity. Of the sym-

physial face itself the dorsal margin is well formed but there is no indication of upper or lower extremity or of ventral margin and there is not much ventral bevelling. The symphysis is in phase III. The symphysial face involves the pubic body and to a slight extent the pubic ramus.

Cebus sp., B. 146, is an animal in the third life period. The epiphysis of the tuber is ossified and fused. From it an extension runs along the subpubic arch but does not reach far. In this specimen the symphysis is entirely pubic and only involves the pubic ramus slightly. From the true symphysis there extends downward an imperfectly ridged narrow strip along the pubic ramus as far as the ischial ramus. In later life this covered by an extension of the ossified ischial tuber epiphysis. This imperfectly ridged strip is characteristic of the Primate above the Lemurs and more extensive reference must be made to it later. On the true symphysial face the dorsal margin is well formed and the dorsal platform has obliterated the ridges and furrows except in the ventral area which shows the commencement of bevelling. As yet there is no indication of either extremity. One therefore assigns the specimen to phase III.

Saimiri (Chrysothrix) oerstedi Rheinhardt, B 341, a female in the fourth life period, shows complete fusion at the symphysis behind but not in front where the ventral margin is not yet completed. The animal is therefore in phase VI of pubic metamorphosis. The symphysial face involves only the pubic body.

CERCOPITHECIDAE

Passing now to the Old World Anthropoidea we glance over the age relationship of the Cercopithecidae before discussing the Anthropoids.

Pithecus rhesus Audebert, B 150, is an animal in the first life period. In its symphysial area the horizontal ridges and furrows are not even well developed. It is not later than phase I. The symphysial face involves pubic body and ramus.

Pithecus rhesus Audebert, B 460, is a female also in the first life period but at the very end for the acetabular elements are in process of uniting. The true symphysis is quite short and is entirely on the body of the pubic bone itself. But from this there extends downward a secondary, roughly ridged narrow prolongation encroaching upon the ischium. The distinction between these two parts of the symphysis has not appeared in the foregoing specimen. It is striking in itself but an additional peculiarity is its transient character. In part at least it is covered by the ischial epiphysis.

Pithecus rhesus Audebert, B 148, not quite so old as the foregoing, shows a practically similar condition. The two may therefore be considered together. The dorsal margin is already fairly well formed and there is an adjoining dorsal platform. There is no definition of extremities and no ventral bevelling. The phase of metamorphosis is therefore III. The narrow ridged prolongation extending as far as the ischium occurs here also. The symphysis extends over the pubic ramus.

Pithecus nemestrinus Linnaeus, B 337 (Fig. 27), is a male at the extreme end of the third life period. The epiphysis for the ischial tuber is now ossified and completely united. The characters of the symphysial area are those just described for B 148 and B 460 except that the lower extremity is forming without the intervention of an epiphysis and the horizontal ridge and furrow system on the face itself is entirely obliterated. The quite secondary nature of the considerable ischial symphysis is clearly shown by its patchiness and irregularity. The specimen is already in phase IV.

Lasiopyga mona Schreber, B 147 (Fig. 31), is a male also at the extreme end of the third life period but in this animal the symphysis is already fused throughout both the true pubic and the secondary ischial portions. We must therefore assign the specimen to phase VII and take up its anomalous position later. (The last vertebral epiphyses in Primates to fuse are those of the lumbar centra: this animal has already slight spondylitis in upper thoracic region—prolongation of period III?.)

Papio hamadryas arabicus Thomas, B 151, is in the fourth life period but the condition of its ischium and symphysis is exactly the same as that of Pithecus nemestrinus B 337 above.

Among the Semnopithecinae two skeletons should receive attention. Of these the first is Pygathrix entellus Dufrèsne, B 158, a female in the later part of the second life period. Its condition, so far as ischium and symphysis go, is again exactly that of Pithecus nemestrinus B 337 except that the lower extremity is less clearly defined. It is at the very beginning of phase IV.

Pygathrix rubicunda Müller, B 622, is another female but this time in the third life period. The symphysial condition is slightly more advanced than that of the last for fusion is beginning between the secondary ischial isolated areas and also in the dorsal part of the true pubic symphysis. The specimen must be placed in phase VII.

From the foregoing survey, fragmentary though it is, we may obtain a very distinct picture of the age relationship of pubic metamorphosis

in the Primates below the Anthropoids. This is represented in detailed form in the graph of the Primates (Fig. 45). In an earlier part of this work (28) I have divided the several phases into three periods. The first includes the post-adolescent phases I, II, III; the second comprises phases IV, V, VI which cover the various processes by which the symphysial outline is built up; the third unites phases VII, VIII, IX, X which typify gradual quiescence and secondary change. In the detailed Primate graph it is seen that the initial phases I, II, III are thrown progressively earlier in relation to the general life periods but that phases IV, V, VI and VII remain much more constant in their age relationship.

SIMIIDAE

In considering the Anthropoids we shall find it most satisfactory to review the giant black Anthropoids—the Gorillas and Chimpanzees—together and first; together because in pelvic form they are very much alike, and first because we have a fairly representative collection which will readily give a standard for comparison with the pelves of the other Anthropoids.

GORILLA AND PAN

Pan satyrus (Stated to be Troglodytes niger), B 168, is a quite young animal in the first life period. There is no attempt at union of the acetabular elements nor any ossification of the epiphysis of the tuber. The symphysial face shows merely the horizontal ridges and furrows typical of the young animal. One may consider it in phase I as one does not yet know at how early an age phase I appears. The symphysial face extends over the pubic body but doubtfully on to the pubic ramus.

Gorilla sp. B 169 (Fig. 33) is in precisely the same condition as regards general skeletal and local symphysial features. In both animals there is a complete milk dentition undisturbed by the permanent teeth. Both would be about two years old upon Keith's computation. (15)

Pan sp. B 347, is an animal in which the permanent dentition is erupting. The third molars have not yet appeared and the milk canines are still all in place. There is no indication of fusion of the acetabular elements nor of ossification of the epiphysis for the tuber. The dorsal symphysial margin is forming and already the dorsal platform has largely obliterated the ridge and furrow system. There is no indication of ventral bevelling or of either extremity and the symphysial face is

continuous with the cartilage covered area extending from the ischial tuber. Indeed one cannot be sure that the symphysial face does not extend slightly on to the ischium. The specimen is in phase III.

Pan sp. B 346 (Fig. 35) is a rather older animal since the milk canines are shed preparatory to the eruption of the permanent teeth. Also there is commencing fusion of the acetabular elements and some slight ossification of the tuberous epiphysis. The dorsal margin and platform are very little advanced beyond the condition in the last. Ventral bevelling has not yet commenced and the extremities are undefined. Indeed the symphysial face is continuous with the ramal cartilage covered surface as in B 347 and therefore may be considered to encroach on the ischium. This specimen is also in phase III.

Pan sp. B 540 (Fig. 37), is at the extreme end of the first life period. The acetabular elements are partly fused. The secondary symphysial extension along the ischio-pubic ramus is very clearly marked and slightly involves the ischium. The dorsal margin of the true symphysial face is largely completed though the dorsal platform is still somewhat small. There is no ventral bevelling and the extremities are not defined. The specimen is therefore assigned to phase III.

Pan sp. B 461, is an animal in which there only remains unfused the ilio-pubic component of the acetabulum. The symphysial condition and extent is the same as in the last. This specimen must also therefore be assigned to phase III.

Pan sp. B 459, is early in the second life period. The epiphysis of the ischial tuber is much more ossified and is even partly united to the main bone. It does not yet extend more than half way towards the lower symphysial extremity. The symphysial condition and extent is unchanged from that of the last. This pubis is classed as phase III.

Pan sp. B 458, is in the second life period. The ischial epiphysis is completely ossified and united; it extends as far as but does not encroach upon the lower symphysial extremity which is now distinctly becoming defined. Ventral bevelling is also apparent but the upper extremity has not become outlined. The specimen is therefore in phase IV. The symphysial face encroaches on the ischium slightly.

Gorilla sp. B 626 (Fig. 34), a female of the third life period, is markedly aberrant for despite its youth the entire symphysial outline is completed and there are even indications of a "rim." There is also considerable ventral secondary excavation. This specimen must be assigned to phase IX and classed as an anomaly to be further investigated. A further evidence of its anomalous condition is indicated by the

fact that the symphysial face is unusually short and extends over the pubic body but only slightly involves the pubic ramus.

Gorilla sp. B 624 (Fig. 36), is a very large male in the fourth life period. Dorsal margin and both extremities are all defined though not strikingly. The dorsal platform and the ventral bevelling have obliterated almost all trace of the ridge and furrow system. A ventral rampart has formed but the ramparts of the two sides are fused together in the middle line to form a single median bar, long, narrow and wedge shaped with its base above. This bar scarcely penetrates between the symphysial faces at all. It is strikingly reminiscent of the corresponding bar—the median disc—found in Marsupials. The specimen must be classed in phase VI. No greater divergence could be found in the detail of pubic metamorphosis than between this and the last specimen. Whereas had this animal lived a little longer, the two halves of the pelvis would have been fused at the pubic symphysis, B 626 has completed its metamorphosis without fusion and apparently without the occurrence of a median bar. These two specimens are the key to the varied appearances which we are about to encounter in the Anthropoids of later life periods. The symphysial face as in the last is rather short. It involves pubic body and ramus.

Pan sp. B 543 (Fig. 38) is specially interesting in contrast with B 624, for it shows the completion of the oval symphysial outline without the assistance of a median disc. The animal was in the fourth life period. The oval outline is complete as just stated but neither extremity is well defined. There is no suggestion of the "rim" which appears later in its lower half but in the upper half it is rough and gives the appearance of a possible approaching fusion. Such a result must not be predicted as being the necessary consequence for irregularity like this is not infrequent after fifty years in Man in whom there is no union. B 543 should not be compared, however, with Man in his sixth life period. Further this irregularity is ventral though it does not encroach upon the ventral margin itself. Secondary erosion appearing first on the symphysial face is rather more dorsally placed. Even comparing B 543 with other specimens of Pan and Gorilla it is obvious that great irregularity need not call for ultimate fusion. The ventral margin has been formed in this specimen directly from the underlying bone. No median disc has been built nor has any attempt been made to form a ventral rampart. The condition of the symphysis in short is precisely similar to the majority of human examples and is assigned to phase

VII. The symphysial face involves the pubis only and does not extend quite to the ischium.

Sometimes, on the contrary, fusion does occur and a very instructive specimen in this regard is Gorilla sp. B 239 (Fig. 39) a female in the fourth life period. As in the last the oval symphysial outline is formed but the extremities are not well defined. The ventral margin has apparently grown up simply by additions to the pubic body itself; there has been no ventral rampart. The growth of the ventral margin however has been quite vigorous and the two pubic bones have just begun to fuse midway along this margin at its extreme ventral edge. In the course of preparation the union has been broken down. Dorsal to the area of fusion is the same irregularity found in the last specimen; only there is in B 239 a somewhat vigorous growth of new bone in the irregular area. This is completely lacking in B 543. The symphysial face involves pubic body and ramus only.

Pan sp. B 629 (Fig. 41), again from the fourth life period, shows complete fusion of the pelvic bones throughout the pubic symphysis. The union has occurred last in the dorsal part and there is no very clear indication of the presence at one time of a median ventral bar or disc. The symphysial face extends over only a part of the pubic ramus.

The three foregoing specimens may all be considered as belonging to phase VII.

Gorilla sp. B 627 (Fig. 43) a female of the fourth life period is of the non-fusing type for although the oval symphysial outline is completed and the extremities are becoming defined there is no vestige of a median disc. The symphysial face is practically smooth and quiescent and should be assigned to phase VIII. The bony ridge for attachment of M. gracilis is well developed in this animal, an unusual condition for even the Anthropoid. The extent of the symphysial face is as in B 629.

Pan sp. B 630, in the fourth life period, is very like the last. The oval outline is complete and the extremities are well defined; the surface is quite quiescent but there has been no attempt at fusion. The gracilis ridge is not developed at all in this animal whose os pubis must be considered in phase VIII. The symphysial face extends over part only of the pubic ramus.

Pan sp. B 628 (Fig. 40), in the fourth life period, is almost a reduplication of B 630 and must also be assigned to phase VIII. The symphysial face is as in the last.

Pan sp. B 171 (Fig. 42) is a most valuable specimen for it illustrates the Anthropoid in the late fifth or early sixth life period. The oval

symphysial outline is complete and there is almost a "rim" formed. The symphysial face itself is markedly irregular from secondary erosion the character of which is entirely different from the condition in such specimens as B 543 and B 239. The dorsal margin is distinctly lipped and from the ventral area there is a considerable outgrowth of new bone. This stimulates somewhat the "bearded" condition of old human symphyses and should be classed in phase X. The symphysial face barely extends even on to the pubic ramus.

PONGO

Pongo pygmaeus Hoppius B 164, is a very young animal at the completion of eruption of the milk dentition. Its os pubis is in phase I or earlier depending upon how far back in the childhood of Man and other mammals one can find a definite pattern in the symphysis. The animal is of course in the first life period. The symphysial face involves pubic body and ramus only.

Pongo pygmaeus B 625, an older animal although still in the first life period, has the milk canines and upper second milk molars in position. Otherwise the dentition consists of permanent teeth and includes the first and second but not the third molars. There is no attempt as yet at union of the acetabular elements although the acetabular rim is distinctly forming. The dorsal symphysial margin is growing and there is even a suggestion of a limited dorsal platform so that the symphysis must be assigned to the border line between phases II and III. The symphysial face has the same limits as in B 164.

Pongo pygmaeus B 623 (Fig. 44) is a male in the fourth life period. The dorsal margin and dorsal platform are well shown. The extremities are not very clearly delimited; the ventral margin is appearing and it is most instructive to examine the specimen closely for it shows admirably how this grows by gradual accretion without the development of a rampart, commencing from below so that the upper part is the last to form. It is therefore in phase VI. The symphysial face does not extend quite so far as to include the ischium.

Our last specimen is Pongo pygmaeus B 172. This is a still older male in the fourth life period. The symphysial outline is completely formed and the symphysial face is quiescent. There is even an indication of a future "rim" round the margin. No ventral rampart has appeared but the ventral margin has grown up by gradual accretion as in the majority of human pelves. One must assign this specimen to late phase VIII. The symphysial face involves only pubic body and ramus.

The record of the Orang, so far as it is indicated by our examples, is quite in harmony with that of the Gorilla and Chimpanzee. We now pass to the Gibbons.

HYLOBATES

Hylobates concolor Harlan (mülleri) B 162, is a quite young animal at the change of dentition. Some of the permanent incisors and the first permanent molars are erupted. The symphysis is of the usual juvenile type which we have classed with phase I temporarily. There is no union of acetabular elements and even the acetabular margin has not begun to develop. The life period is clearly the first. The symphysis doubtfully involves the ischium.

A much older animal though still in the first life period is Hylobates hoolock B 159 (Fig. 30). In this the ridge and furrow system is very clear although the dorsal margin is beginning to grow quite vigorously. Neither extremity is even indicated and there is no ventral bevelling. The specimen must be assigned to phase II. The symphysial face involves the ischium to a small extent.

Hylobates concolor B 160 is a male in the early fourth period for the epiphysial lines of the vertebral centra are still visible. The two halves of the pelvis are united but quite recently for in the middle of the dorsal pubic area alone is there so complete fusion that the line of union cannot be made out. The entire absence of any ventral rampart or median disc can still be definitely asserted and as in the other specimens of Hylobates the ischium enters into the formation of the symphysis only at its extreme lowest part, and this is secondary as in the Cercopithecidae. The specimen belongs to phase VII.

Hylobates concolor B 161 (Fig. 32), is a female in the fourth life period in which there is complete fusion at the symphysis into which the ischium does not enter at all. The ischial rami approximate each other and are united by a fibrous band. One must assign this pubis to phase VII or later.

Our Gibbon records then, scanty as they are, fall more into line with the age relationships of the other Anthropoids than they do with those of the Cercopithecidae, although the symphysial face in its extent resembles the latter more closely.

In the graph are shown at a glance the age relationships of the various families and subfamilies of the Primates including Man (Fig. 45). The number examined, though considerable in the aggregate, is small when divided thus and doubtless many minor alterations would have to

be made if a much greater number were available. Leaving phase I out of account as being of less value and definition than the others the commencement of pubic metamorphosis occurs progressively earlier as we ascend the scale of the Primates until the Cercopithecidae are reached. This precocity is not long maintained and during phases IV, V, VI all the curves approach each other more closely. It is not yet clear as to why Man does not share in this early precocity.

The relationship of the Primate curve to that of other mammalian orders is laid out in the same figure.

The Relation of Ischium to Symphysis

At several stages of the foregoing discussion the rôle played by the ischium in symphysis formation has come in for notice. At this point it is well to review the subject as a whole with the object of ascertaining the evidence relating to the evolution of this area in the Mammalia.

In Monotremes as in the mammal-like reptiles the symphysis consists in almost equal parts of pubis and ischium but so far as all other mammals are concerned there is a very different composition of the symphysis. The length of the symphysis in most Marsupials gives one the impression at first that the ischium enters largely into its formation. This is not the case; at most the ischium contributes merely the very lowest portion of the actual symphysis. The lower nodule (interpubic bone of Owen) by its fusion with the two sides of the ischial portions of the ischio-pubic rami gathers the ischia, as it were, into the symphysial area. In some animals, Petaurus and the Kangaroos for example, the extent of the symphysis beyond the lowest level of the obturator foramina indicates considerable involvement of the ischia but as a rule the ischia do no more than lodge the lower nodule.

In the Rodents we have seen that certainly no more than this occurs and in most mammals the ischia take no part in the symphysial formation even if it be long. Many Rodents have a rudimentary symphysis or none at all. In this order, as in the Lipotyphla among the Insectivores evolution is all towards reduction of the symphysial length and eventually to its total elimination.

In the Menotyphla as represented by Tupaia the symphysis is coterminous with the limits of the pubic body and ramus; it does not infringe upon the ischia.

In the Carnivores there is an elongation which involves the ischia slightly, mainly as a result of their fusion with the lower nodule.

In the Ungulates the true symphysis is almost entirely confined to the body of the pubis. Involvement of most of the pubic and of the

ischial portions of the ramus is obviously secondary and due to approximation of the rami and binding of them together by the median bar of bone rather than to genuine co-ossification.

All other orders except the Primates may be passed over as giving no help because of reduction or elimination of the symphysis.

In the Primates so far as the Lemurs, the giant Anthropoids and Man are concerned the symphysis involves the body and part of the ramal portion of the pubis. In the Platyrrhinae there is apt to be a slight encroachment on the ischium but nothing like so pronounced as in the Cercopithecidae. In both subfamilies of Old World Monkeys although the true symphysis is entirely or almost entirely limited to the pubic body and the pubic rami may be actually little involved an approximation of the ischia is apt to occur with secondary union. In Hylobates also the elongation of the apparent symphysis takes place from secondary involvement of the ischia.

The sum total of this evidence is that so far as Marsupials and Placentals are concerned involvement of the ischium in the symphysis is slight. It occurs only in pelves in which fusion takes place at the symphysis and indeed in only a certain number of this type. The replacement by a single median chain of ossification centers of the original bilateral ossification centers for ventral margin and extremities of the symphysial face is followed by fusion at the symphysis and is quite in accord with the reptilian ancestry. In some of these pelves, the Marsupials and Carnivores for example the symphysis only slightly involves the ischia. In the Ungulates involvement of the ischia is supernumerary and not due to real inclusion in the symphysial area.

Evolution of the Eutherian Symphysis

The characters of the actual primitive mammalian symphysis can only be learned from fossil material but in much of this the symphysial area is missing. Especially is this true of the vitally important specimens. Hence it will not be amiss to state what can be discerned from the study of recent skeletons. Two alternatives only can be supposed regarding the primitive Eutherian symphysis. One is that originally the symphysis was long and involved both pubis and ischium. The other is that the symphysis was very short and restricted to the pubis. There is no justification at all for the second view so far as Reptilia are concerned. The mammal-like reptiles of the Permian and Triassic all showed the plate-like symphysial area characteristic of reptiles in general and still represented in existing Monotremata. Marsupials

(with the exception of the very specialized Notoryctes), most Carnivores, some Rodents and a few Insectivores display symphyses in which the ischium is involved but to no great extent. Indeed the involvement of the ischia is largely associated with the occurrence of a median ossification which we have named the lower nodule. In no other Eutheria does one find the complete ischio-pubic symphysis with all the factors which build up the symphysial area. Even in these the pubic part is obviously the more important; it has a greater dorsoventral depth and the details of its formation and ultimate fusion differ from those of the ischial portion.

In the Ungulates which retain the long ischio-pubic symphysis the ischial portion has become supernumerary and presents a symphysial face which is quite rudimentary and easily distinguished from the pubic part. The pubic symphysial face, on the other hand, is large and becomes the chief bond of union between the two pelvic halves. In spite of reduction of the ischial symphysis the Ungulates retain the lower nodule and the long median bar although since these have lost their original intimate relation to the ischial symphysial face, the bone formed by them unites with the symphysial area comparatively late. This is understood at once when one recalls that the union takes place first in the lower (ischial) portion. Thus in young animals the ossified median bar with the lower nodule is apt to be lost in maceration.

In Rodents there is a well marked tendency to shortening of the symphysis. Even though the actual length of the symphysis be rather great it may be comprised in its entirety by the pubis. In this order are symphyses retaining the lower nodule as in Castor (Anderson, 2); symphyses in which the lower nodule ossifies from two distinct centers (Dolichotis B 267); symphyses in which the lower nodule does not exist as such but is replaced by a bilateral ossification, apparently the ventral extremity of the ischial tuber epiphysis (Trichys B 264). There are other types of symphysis limited to the pubis showing an ever greater shortness until one reaches the type of pelvis in which no symphysis occurs at all.

In the Insectivores and their allies the same varieties of symphysis are found, but not with the same gradual gradations, as occur in Rodents.

Edentates show an extremely short symphysis which nevertheless presents distinct indications that it once was more typically Eutherian.

In Primates there is developed a median bar but no lower nodule. The symphysial faces are completed, as in Trichys, by extension of the epiphysis for the tuber. The upper nodule is irregular in many ways

and is always bilateral. The symphysis involves only the pubis except doubtfully in a few representatives of various Families (see pp. 393-394) the most notable instance being Pan. In the giant Anthropoids frequently and in Man always fusion of the two pelvic halves at the symphysis is lacking. Upper nodule, median bar and lower nodule are represented by bilateral ossifications in the adjacent soft parts along the ischio-pubic ramus.

The foregoing summary of facts already presented in the body of this paper indicates clearly that quite early in the history of the pre-mammals or the primitive mammals a marked differentiation occurred at the symphysis. Instead of the ischium and pubis playing equal parts in the symphysis the pubis became vastly more important for some reason regarding which we know nothing at present. Participation by the ischium, on the contrary, greatly dwindled until merely a fraction was left. This resulted in a separation of the ischia of opposite sides. Perhaps the lower nodule disappears. Perhaps its originally bilateral centers become separated and form the lower extremities of the symphysial faces of the two sides. In favor of this is, first, the case of Dolichotis B 267, with its bilateral ossification of the lower nodule. Secondly many Primates, including Man, show a bilateral ossification completing the symphysial face below.

Further stages in the evolution of the symphysis occur in the Primates. In many giant Anthropoids and in Man there is failure of the symphysis to unite at phase VII. On the contrary there is an obviously secondary union of ischia in Cercopithecidae and in Hylobates to some extent. This type differs absolutely from the condition in Ungulates in that there is no vestige of a lower median nodule. Continued shortening of the symphysis has taken place in Rodentia, Insectivora and Edentata, in other specialized orders and in specialized genera of more typical orders until ultimately the symphysis is absent altogether.

In the above manner it is a simple matter to trace out the history of the mammalian symphysis from the primitive and typical Eutherian form which engages the ischium to a small extent only and is still represented in Marsupialia, Carnivora, menotyphlous Insectivora and some Rodentia. The Ungulates which we have discussed show a symphysis plainly indicating its derivation from a primitive type with these features. The Primates must have early broken away from the typical Eutherian stock and developed a symphysial area such as is exhibited by Microcebus B 434. From this can easily be derived a type like that of Man and some giant Anthropoids on the one hand, and

a type like that of the Cercopithecidae (e. g. Pithecus nemestrinus B 337) on the other. No other interpretation of the facts seems to me possible. It may be objected that one should not derive a bilateral structure from a median one. This is correct but as has been shown the median nature of the nodules and median bar is itself secondary. We are dealing with conditions in which this secondary median structure is now breaking up into its component parts. The relation of this to the human symphysis is reserved for part VI of the present memoir.

Principles of Mammalian Pubic Metamorphosis

In the previous section have been noted the stages in specialization of the symphysial area and a view of symphysial evolution has been put forward. In the body of the memoir we have made frequent reference to successive phases of pubic metamorphosis and have observed that the phases as originally outlined for Man have been almost equally useful for mammals in general .

In the young mammal in the earlier part of the first life period the symphysial face is a gently rounded bony surface with no definite margins and apparently continuous on to the ischial ramus. It is of subequal ventro-dorsal diameter throughout. The horizontal bony ridges and furrows are either not present or very slightly marked. A typical example is Pithecus rhesus Audebert B 150. Animals with rudimentary symphyses like Galeopithecus or Gymnura never develop any features of the surface characteristic of later phases. It is often difficult to distinguish between this infantile stage and the pubescent phase I, hence for present purposes of convenience such specimens are included as "Phase I or earlier."

Phase II presents the same general similarity to phase I as in Man and is an intermediate stage towards the more definite phase III which, while closely resembling that of Man presents certain additional or alternative features. The dorsal margin develops first in the upper part and is quickly followed by the appearance of a dorsal platform adjacent. Ventral to these features are the remnants of the horizontal ridges and furrows. The lower symphysial face lingers behind the upper in differentiation and at the stage when the upper part exhibits the features just enumerated may still show the complete and unchanged ridges and furrows. Such a specimen is Pithecus rhesus B 460. Another feature is the late appearance of ventral bevelling. In Man we are accustomed to expect this in the third phase but in mammals generally it may not take place until shortly before the development of the ventral margin (median bar).

Phases IV and V show the same general characters as in Man and also show the same confusion. The upper extremity usually becomes defined second but may be indicated at the same time as or even before the lower. This confusion in Man caused me to hesitate for a long time before determining the phase relationships as I finally submitted them in my first paper (26). It is interesting to note that the same confusion occurs in other animals. I am inclined to consider this a secondary phenomenon, possibly retrogressive, the more primitive condition being that in which definition of the lower extremity distinctly precedes delimitation of the upper. In phase V ventral rarefaction can always be found although sometimes molecular in appearance.

Phase VI is the stage of development of the median bar in pelves in which there is a single median chain of ossification centers. This takes place by extension from the upper and lower nodules. Usually it becomes fused with the underlying ventral part of the symphysial face almost at once and thus produces the ventral margin corresponding to the ventral rampart of some human symphyses. But in the Ungulates the median bar ossifies very early, probably at about phase III, and remains ununited until much later. There is correspondingly a complete absence of ventral bevelling until just before phase VI commences in these animals. It is difficult to say whether the metamorphosis typical of Ungulates is an exaggerated example of what I have called the sporadic attempt at ventral margin formation which is apt to occur during phase V in Man. The processes are undoubtedly the same but compared with most mammals this stage of metamorphosis is greatly retarded in Man whereas it is accelerated in Ungulates. One would hesitate therefore to compare the two processes at all closely. One may ask if any fusion of the two sides takes place during phase VI since the median bar rapidly unites with the underlying bone. It certainly does but through the medium of the median bar only. This fusion may take place before the median bar itself is completely formed. No fusion of the symphysis behind takes place during this phase.

Phase VII in Man is significant because it is during this phase that changes take place in the symphysial face itself. The change which occurs must necessarily differ according to whether the symphysial faces are going to fuse or to remain separate. If, as in Man, they remain separate the change is one of settling down into quiescence. If on the other hand fusion is to occur it will take place at this stage. This fact cannot be too strongly emphasized. Union of the two pelvic halves invariably occurs at this stage if the fusion is normal and not patho-

logical. Some animals are particularly appropriate for the study of this problem, notably the giant Anthropoids. In certain of these fusion does occur and our records show that union took place always at this particular stage. In others fusion does not occur and the symphysial faces of these specimens have undergone changes which are typical also of Man.

Phases VIII and IX are indistinguishable in mammals whose symphysial faces unite. They can be represented by the sign phase VII+.

Phase X is as well marked in other mammals as it is in Man. It presents the same characteristics and is just as easily differentiated from phases VI and VII as in human bones.

It will be seen that there are no strikingly new features to be recorded for mammals generally beyond those already laid down for the investigation of the human symphysis. There is therefore no need for a separate tabulation of phases.

FATE OF THE MEDIAN BAR

Three distinct types of symphysis are to be found among the Eutheria.

1. Those in which the two pelvic halves ultimately (in phase VII) fuse together at the symphysis.

2. Those in which, as in Man, the two pelvic halves remain separate throughout life but articulate together by symphysial bony surfaces.

3. Those in which the two pelvic halves do not meet at the symphysis but either are united with each other simply by a ligamentous band, the bony surfaces not touching, or are more or less widely separated and have no connection at all.

When one examines in detail the features of metamorphosis of these three groups certain significant differences emerge. The third type is plainly retrogressive. No accessory ossification centers occur in the area of these symphyses; the symphysial faces, if they are present at all, are merely rounded cancellous masses of bone covered by the merest shell of compact tissue and without definite pattern or margins. An example in which symphysial faces do occur, yet do not articulate is Gymnura. The Edentates possess symphyses which are apparently aberrant forms of the first type. Their symphyses must therefore be considered after the more usual ones.

The second type is found in Man and in some examples, but not all, of the giant Anthropoids. As a rule in these cases the symphysial outline grows up by gradual accretion of bony substance; first the dorsal margin, next the lower extremity followed almost at once by the upper,

and last of all by the ventral margin. Further, the development of these margins takes place without apparent relation to any epiphysial ossification along the ischio-pubic ramus. It will be our aim in the succeeding section of this monograph (Part VI) to present evidence for the explanation of the evolution of this type of metamorphosis from a form in which bony development from epiphysial or secondary centers occurs along the ischio-pubic ramus up to and into the areas of the symphysis. These represent the median bar with its nodules as seen in other orders.

We now pass to the first type of symphysis, namely that in which fusion of the two sides takes place during Phase VII. Eliminating the aberrant symphyses of the Edentates, the Ungulates, the Cercopithecidae and Hylobates we find a short form and a long form. The former is represented by some examples of the giant Anthropoids among other mammals, and the latter by Carnivores and Marsupials. The distinction between these two is briefly summarized in the character of the lower symphysial extremity. In the giant Anthropoids cited the lower extremity forms as in the majority of human specimens by the gradual development of a definitive margin. In the long or typical Eutherian form it develops by the appearance of a single median mass of bone (the triangular ossicle of Owen) which fuses with the ischia and thus completes the symphysis below. At first these seem far removed from each other although no doubt, if the entire ossification could be examined in a fortunate series, the lower nodule (interpubic bone) would be found to ossify from a double center. The clue to the relationship of the two forms, the long and the short, is given by certain Rodents, for example Dolichotis B 267, and Trichys B 264 and by Microcebus B 434. In this specimen of Microcebus the independent bony centers for the formation of upper and lower extremities are clearly seen (Fig. 26) and there is no doubt that the condition of the giant Anthropoid represents this in retrogressive form. In Dolichotis (Fig. 12) the lower nodule is bilateral and composed of two separate ossification centers. The Rodent symphysis like that of Microcebus is precisely where, upon phylogenetic grounds, one would expect to find evidence in favor of bilateral origin if such evidence there be. We are fortunate in the possession of these pelves which give the necessary data.

The evidence presented for the lower nodule may be applied to the elucidation of the median bar itself. To obtain direct evidence of the bilateral nature of this feature through a double ossification in symphyses where ultimate fusion takes place does not appear to be a profitable task. Yet the evidence for the lower nodule (or extremity)

combined with that for the upper extremity in Microcebus and for the ventral rampart in Man (see part VI later) indicates clearly the bilateral origin. One must infer therefore that the median bar with its associated expanded upper and lower nodules is a secondary though ancient phenomenon and that Dolichotis and Microcebus show a breaking down into the original elements. It also follows that the type of symphysis presented by Man is retrogressive and that the symphysis of the giant Anthropoids is likewise retrogressive though not to quite so advanced a degree.

In the Ungulates we have apparently a type of symphysis in which the union of the ischia is supernumerary and now more or less accidental through approximation. The condition is undoubtedly secondary and the union certainly seems almost hap-hazard in consequence of approximation. But there are features which clearly indicate the ancestral history of the present appearance. A distinct median bar occurs at least in the Artiodactyla, and although a bar is rudimentary or absent in the Perissodactyla both orders possess a definite lower nodule. This lower nodule or interpubic bone is a certain indication of a once typical Eutherian symphysis especially when accompanied by a median bar. Since the lower nodule in the Ungulates unites the ischia it follows that the symphysis at one time included the entire pubis, both body and ramus, and further extended to the ischium. More recently the true symphysis became confined to the pubic body with resultant specializations which have already been discussed. The part of the symphysis formed by the ischio-pubic rami dwindled in importance and became rudimentary, but the lower nodule maintained its original position. We conclude therefore that the Ungulate symphysis passed through a typical Eutherian stage.

Far different is the symphysis of the Ceropithecidae and of Hylobates, although here again we have the union of pubic and to a small extent of ischial rami. The final result is not unlike that in Ungulates, but the two types are widely different in their history. There is no lower nodule in relation to the ischia of these animals. There is no lower nodule at all but its bilateral representative, if it occur, is found forming the lower extremity of the true symphysial face on the body or at lowest on the ramus of the pubis as in Microcebus. The union of the greater part of the pubic rami and also of the ischial rami, if these be united, is certainly a secondary one through approximation and obtains at a lower level than the site of the representative of the lower nodule or interpubic bone. There must be no confusion between this type and

that of the Ungulates. The Cercopitheque symphysis has developed after the Primate symphysis became fixed. It is not a direct derivative of the typical Eutherian symphysis.

Finally concerning the Edentates it must be pointed out that since they present a lower nodule even in their short symphysis, they must have passed through a stage corresponding to the first type of symphysis where, in association with length of the symphysis and development of a median bar the lower nodule has been formed. As the symphysis became shorter in retrogression the lower nodule remained as the earmark of the former condition. Judging the Lipotyphla in light of the Menotyphla these also must have passed through the general Eutherian stage represented by type 1, but they have become vastly more specialized than the Edentata in this regard. Rodents with an extremely short or missing symphysis fall into the same category.

THE INFLUENCE OF AGE UPON EXTENT OF THE SYMPHYSIS

In the last chapter we have observed that the Primate symphysis early diverged from the typical Eutherian stage. We have also noted that the Cercopitheque extension, by which the ischium is involved in the symphysis, is a quite late modification after the Primate type of symphysis became fixed. It is instructive to inquire into this peculiar extension. I have therefore arranged in tabular form information regarding extent of the symphysial area in relation to successive life periods. In this manner one may see at a glance the bearing of age.

Genus.	Sex.	Number.	Life Period. 1	2	3	4	5	6
			Lemuroidea					
Microcebus	M.	B 434		Body				
Nycticebus	M.	B 136		Body				
Tarsius	?.	B 135				Body		
Lemur	?.	B 138		Body				
Lemur	F.	B 197				Ramus sl.		
Lemur	F.	B 344				Ramus sl.		
Lepidolemur	M.	B 345				? Ramus sl.		
Lemur	M.	B 137				? Ramus sl.		
Indris	M.	B 343				Ischium		
Daubentonia	M.	B 198				Ramus		

Genus.	Sex.	Number.	Life Period. 1	2	3	4	5	6
			Cebidae.					
Ateleus	M.	B 141		Ramus				
Cebus	M.	B 142		Ramus sl.				
Aotus	F.	B 342		? Isch.				
Alouatta	M.	B 340			Ramus sl.			
Cebus	?.	B 146			Ramus sl.			
Saimiri	F.	B 341			Body			
			Cercopithecidae.					
Pithecus	?.	B 150	Ramus					
Pithecus	F.	B 460	Body					
Pithecus	?	B 148	Ramus					
Pithecus	M.	B 337			Isch.			
Lasiopyga	M.	B 147			Isch.			
Papio	M?	B 151			Isch.			
Pygathrix	F.	B 158		Isch.				
Pygathrix	F.	B 622			Isch.			
			Anthropoidea.					
Hylobates	?	B 162	? Isch.					
Hylobates	M.	B 159	Isch.					
Hylobates	M.	B 160				Isch.		
Hylobates	F.	B 161				Ramus		
Pongo	?	B 164	Ramus					
Pongo	?	B 625	Ramus					
Pongo	M.	B 623				Ramus		
Pongo	M.	B 172				Ramus		
Pan	?	B 168	? Ramus					
Gorilla	?	B 169	? Ramus					
Pan	F?	B 347	? Isch.					
Pan	F?	B 346	? Isch.					
Pan	M.	B 540	Isch.					
Pan	F?	B 461	Isch.					
Pan	F.	B 459		Isch.				
Pan	F.	B 458		Isch.				
Gorilla	F.	B 626			Ramus sl.			
Gorilla	M.	B 624			Ramus			
Pan	M?	B 543				Ramus		
Gorilla	F.	B 239				Ramus		
Pan	M.	B 629				Ramus		
Gorilla	F.	B 627				Ramus		
Pan	M.	B 630				Ramus		
Pan	M.	B 628				Ramus		
Pan	F.	B 171						Ramus sl.

In the foregoing table contractions are used as follows:
Body means that the symphysis is confined to the pubic body;
Ramus means that the symphysis extends on to the pubic ramus;
sl. means slightly;
Isch. means extension of symphysis on to ischium.
The table shows several significant facts.

In the Lemurs the symphysis is practically limited to the pubic body except in Indris and Daubentonia. The loss of the tail and the habits of Indris may have some important relation to this unusual condition. Daubentonia in many ways is closely related to the Indrisinae and perhaps this accounts for the extension which involves much more of the pubic ramus than in other Lemurs, although, as previously stated the symphysial area seems to have no definite taxonomic value.

In the New World Monkeys extension of the symphysis to the pubic ramus has become fairly fixed, but it is only slight.

In the Old World Monkeys and Apes extension to the pubic ramus occurs quite early in life. Somewhat later the ischia also participate in the symphysis. The obviously secondary nature of this involvement is clearly shown in Fig. 27 which is a photograph of Pithecus nemestrinus B 337. With involvement of the ischia there seems to develop a curvature of the symphysial area with ventral convexity. It really appears as if this is an extension occurring between the first and second life periods in these animals. If this is ultimately proved to be the case it will be an astonishing acquired character since in Hylobates it occurs much earlier.

Hylobates represents the maximum Primate involvement of ischium.

Again in Pan there is undoubted ischial involvement in some but not in all instances. It is much less than in Hylobates. Sex has no relation to this extension so far as our examples go.

In Gorilla and Pongo the symphysis does not involve the ischium.

In general one must admit that there is some evidence of extension of the symphysis in various Primates during life, and that this extension takes place somewhere about the beginning of the second life period. The evidence is the following.

In the Cercopithecidae specimens show definitely a limitation of the true symphysis to the pubic body (though it may slightly encroach upon the pubic ramus). This symphysial face is oval with the long axis vertical and is distinctly marked off from the secondary symphysis resulting from approximation as illustrated in Pithecus nemestrinus B 337 (Fig. 27). The appearance of this specimen is quite typical of

the others. Further, in young specimens there is no indication of the secondary symphysis but there is evidence of the presence of an ischio-pubic epiphysis in the extension of transverse ridges along the ischio-pubic ramus for an indefinite distance (e. g. Pithecus rhesus B 460 see p. 376). This epiphysial surface could not be mistaken for the symphysial face because it is much narrower and between the two is a pretty definite demarcation. The third piece of evidence is the occurrence of this same epiphysial marking in Pan (see Fig. 37) in some specimens of which symphysial involvement of the ischium takes place. My belief is that involvement of the ischium in Pan is brought about by extension of the symphysial face to include a part of this epiphysial mass. There does not seem to be the actual bending which occurs in the Cercopithecidae.

Looking over the table one might imagine that the Lemurs also confirm this view but this is not so. The younger specimens almost all belong to a group which presents a typically short symphysis.

If then age has any bearing upon the length of the symphysis it is shown only in the Cercopithecidae and to a less extent in Hylobates and Pan. I have seen no evidence in any other mammals.

RELATION OF SEX TO THE MAMMALIAN SYMPHYSIS

There is a general impression, applying to Man as well as to other mammals, that sex bears a rather constant relation to the form of the symphysial face. It is said that the long symphysis is characteristic of the male, the short characteristic of the female. The problem, so far as it affects the form of the human symphysis has not yet been touched upon in the present work but one could not leave this section of the memoir without referring to the sex question both as regards form and metamorphosis.

As to metamorphosis a vastly greater amount of material would be necessary to justify any conclusions whatever. Unless greater sexual difference were to occur than is present in Man, and on general grounds this is certainly not to be expected, we should require almost as many skeletons of known age and of one mammalian family at least as were used in the survey of human material, before a definite statement could be made. In the present investigation I have found nothing which would even indicate a sexual difference in mammalian pubic metamorphosis.

We pass then to the consideration of form. In the Ungulates it has been pointed out that there is a very definite sexual distinction in shape of the symphysial face; this is even more pronounced in the Perisso-

dactyla than in the Artiodactyla. I am not able to speak regarding other Ungulate orders. In the male the symphysial face is biconvex; in the female, owing to flattening of the pelvic aspect of the symphysial area, the symphysial face is almost plano-convex, the convexity being directed ventrally. In the Mare the symphysial face is even concavo-convex. The distinction between the sexes is shown by a comparison of Figs. 13 and 14 which illustrate the symphysial face in Odocoileus virginianus.

Nowhere else among mammals does one find this clear distinction nor does the symphysial face itself by its pattern indicate sex in any mammalian order. There is one feature which often indicates sex though not very strongly. When discussing the position of the pubic tubercle in relation to sex in Man (26) I pointed out that the most characteristic sex feature in this part of the bone is neither the prominence nor degree of isolation of the tubercle from the symphysis but rather the massiveness of the upper border of the pubic bone. In other mammals, as in Man, this feature again stands out. It is not very well marked and even in the Anthropoids it may be quite equivocal. It is present in greater degree in Ungulates, and this fact gives a clue to its significance. In all mammals except Ungulates the symphysial face is long and comparatively narrow. In Man it may be equally narrow and is usually not broad. In Ungulates on the other hand the symphysial face is short and is confined to the upper part of the pubic body. The great dorso-ventral depth of the pubis in the male Ungulate is naturally reflected therefore in the massive upper pubic margin. The greatly reduced dorso-ventral depth in the female is likewise reflected in the sharp, or at least narrow, upper pubic margin. We have seen that the sexual difference is better marked in the symphysial face of Equus than in any other of our Ungulates. It is therefore not surprising that we find the greatest sex difference in the upper pubic margin of this animal also. In Man this sex distinction is not invariable; often it is quite equivocal. One must expect this since the symphysial face varies so much in dorso-ventral depth, and quite without relation to sex.

The actual or relative length of the symphysial face alone remains for discussion. At a later date the results for Man will be presented. The actual length must of course be checked up against the individual as a whole and the relative length against some pelvic standard. Neither method meets so far with any measure of success. But if there is difficulty in judging of the relation to sex in the symphysial length in Man

the difficulty is greatly enhanced in other mammals. It is true that V. D. Broek has, in 1911, depicted sexual differences in the symphysial length of various Primates (3). The statements and the figures do not take into account the age or size of the animals and the photographs are not clear enough to enable me to draw any conclusions as to these points. There being no standard used for estimating the proportional length of the symphysis, and in the absence of sufficient data regarding the skeletons themselves it is impossible to use the work in the present investigation. I have seen no real evidence to justify belief in a sexual factor in symphysial length. So far as the Primates are concerned the table on pp. 393-394 shows that even involvement of the ischium, which surely would bring about the most striking difference in symphysial length, bears no definite relation to sex. An "appreciation" of sex founded upon symphysial length is mere guess work.

GRAPHIC REPRESENTATION OF AGE RELATIONSHIPS

The mass of information contained in the body of this paper relating to pubic metamorphosis and life periods must be reduced to simple form before the salient facts become obvious. We have noted that no new statement of phases has been rendered necessary through the study of the Mammalia. The phases as arranged for Man are equally exemplified by other mammals. Two features however have to be kept in mind. In the Monotremes there are no epiphyses on the centra of presacral vertebrae and hence phase III drops out of consideration. Further, in most mammals which possess a fairly typical Eutherian symphysis, the two pelvic halves fuse in the midventral line. I have produced evidence that this fusion always takes place in phase VII or at the extreme end of phase VI. Without this clear understanding one would have difficulty in placing many of these pelves as regards phase.

With these facts in mind I have gone over in detail all the skeletons mentioned in this paper and have plotted out on millimeter paper each skeleton as regards the phase of its pubic metamorphosis and its position in the appropriate life period. Using smoothed graphs I have reduced them all to the single graph shown in Fig. 45 which well repays a little careful study. Although I have warned against the assumption that life period limitations necessarily occur at the same stages relative to either the total life span or any type of activity of the animal, yet since we are comparing all results with those obtained in the study of Man I have arranged the life period limits at intervals corresponding to those

found in Man. This I believe to be justifiable in the circumstances and in any case there is no other standard at present available.

The graph, in brief, shows that probably all mammals with the exception of Man commence to show active pubic metamorphosis during the first life period; that the Marsupials (and the Monotremes) complete their pubic metamorphosis, at least to phase VII, before the end of the second period; that they are followed a little later by the Rodents and by the very atypical Ungulates; that the Carnivores and the Primates pursue a very similar course and their curves practically parallel each other throughout the metamorphosis; and finally that Man lags behind in its commencement and during phases VII, VIII and IX. We must examine these points more closely.

Why the Marsupials should so greatly precede the other orders in completion of their pubic metamorphosis finds no explanation here. It is noteworthy that the Monotremes also complete metamorphosis very early. The Edentates reach phase VII before or early in the third life period. They are not quite comparable with the Marsupials for their metamorphosis starts late and progresses rapidly. It is more probably correct to interpret this phenomenon as related to the aberrant and very short symphysis. Among the Marsupials our three specimens of Phascolomys show some retardation in speed of metamorphosis.

Rodents, as one would expect from the very various character of their symphyses, show the greatest number of deviations from the precise line of the curve. Trichys is accelerated and Mus (but not Hydromys) is retarded.

The aberrant Ungulates pursue a course of their own and among them Capra shows some retardation. The specialization of the symphysial face in these animals renders absolute identification of the early phases very difficult.

Regarding the Carnivores there is no special comment to make. They are remarkably harmonious in their age relationship.

In the Primates the difference between the curves of the various groups may be more apparent than real. They may be partly due to the comparatively small number examined. The close connection between curves for Cercopithecidae and Anthropoidea is interesting. If anything Man falls nearer the Lemurs in this graph but I am not inclined to place much weight upon this.

The black dots represent anomalies among Primates. It is significant that these always show acceleration and that they all fall within the range of the Eutheria and not outside it. Regarding the human anoma-

lies we shall have more to say in part VI. The black circles simply indicate the sites of the commoner time anomalies.

NATURE OF THE ANTHROPOID SYMPHYSIS

The striking feature of the giant Anthropoid symphysis is that it may complete its metamorphosis by one of two methods. In one the metamorphosis is very similar to that found in the majority of human pelves. The phases are the same of course but in addition there are the irregularity in time of definition of the upper extremity, the building up of the ventral margin by gradual accretion and without any sign of a ventral rampart, the development of a "rim" indicating phase IX, and the occurrence of senile changes of an identical kind. Since no other mammal presents features so similar in detail we may take it that the method of evolution of the human symphysis and this type of Anthropoid symphysis must have been the same.

The second type of symphysis brings the giant Anthropoid into relation with other Primates. In it there is formed a median bar ventral in position and expanded above but tapering below. By means of this first but later directly the two pelvic halves become fused in phase VII. In some way the presence of this median bar is related to the fusion which never takes place in any specimen not developing a median bar. I have already claimed that the original ossification must have been bilateral and that the median bar and indeed the fusion must be secondary though ancient features. Nevertheless the second type of Anthropoid symphysis is more primitive than the first; it is the result of an effort to follow the typical Eutherian course, and it failed because in no circumstances can a single median lower nodule be developed. It indicates why the ischial union of the Cercopithecidae is so certainly secondary.

But if the second type of symphysis is a specialization from the typical Eutherian form, the first, in its present form, is equally certainly a retrogressive condition. No indication of epiphysial formation is visible in it at all.

The relation of age and sex to form in the Anthropoid symphysis has been discussed in previous chapters.

The striking difference between the symphysial area in Hylobates and that of other Anthropoids is sufficiently evident. The symphysis of Hylobates is really an intensified form of Old World Ape symphysis. This simply confirms the position of Hylobates as ascertained by many other and much more important morphological features.

NATURE OF THE BONY METAMORPHOSIS AT THE MAMMALIAN SYMPHYSIS PUBIS

Throughout this work the relationship of the symphysial changes to an epiphysial formation has been alluded to and commented upon, so that, although the final and complete demonstration must be left to part VI, it is advisable to recall briefly the points to which allusion has been made from time to time.

The symphysial face itself resembles the diaphysial side of a diaphyso-epiphysial plane in the earlier phases of metamorphosis. The loss of this appearance with its billowy ridges commences behind. As the ossification of the soft tissue ventrally proceeds and forms successively the lower extremity or nodule, the upper extremity or nodule, and the ventral rampart or median bar, which are all quite obviously of an epiphysial nature, the ventral part of the symphysial face changes in its structure preliminary to ultimate fusion with these epiphysial formations. In the Marsupial the median bar is an actual disc penetrating the tissues between the symphysial faces almost as far as their dorsal limit. This is the fused "epiphysis" at its greatest development.

The irregularity in occurrence, in time of appearance, and in size and shape of the upper bony nodule indicate its condition to be that of a retrogressive epiphysis. Sometimes in Man it extends as far as the pubic tubercle but most often not.

The relation of the lower extremity or of the lower nodule to the epiphysis of the ischial tuber has been often commented upon and this clearly indicates its condition.

The methods of formation of the ventral margin, ventral rampart and ventral or median bar plainly illustrate the relation of this feature to an epiphysis more or less modified.

There is a tendency to failure of completion of the ventral margin, rampart or bar and of the upper extremity or nodule. This tendency is common in all Primates and Carnivores and even occurs sometimes in Ungulates. Its occurrence has been noted in Man. This common tendency is none other than a failure of ossification in a retrogressive epiphysis.

Altogether these features make plain the relation of symphysial bony metamorphosis to a modified epiphysis.

Two other features common to the symphyses closely related on the graph (Fig. 45), namely the Carnivores, Primates and Man are first; the fact of fusion (excluding Man) taking place invariably at the same period, and secondly the similarity in type and position of secondary or senile changes. These invariably occur first either at the upper part

of the ventral margin or on the dorsal part of the symphysial face. Ultimately the process extends over both areas (see Figs. 19, 25, 42).

SUMMARY

1. This paper forms a portion of a memoir upon the anatomy of the symphysial region of the os pubis.

2. The evolution of the symphysial area in Eutherian mammals is studied. It is shown that the Eutherian symphysis diverged early from the reptilian form illustrated by the Permian mammal-like reptiles and retained in existing Monotremes. The central feature of this divergence was the emphasis of the pubic portion of the symphysis with a correlated diminution of the ischial part. In certain forms, of which Man is one, the primitively fused symphysis is resolved again into two non-uniting components. Further changes go on in more specialized symphyses until no symphysis remains.

3. The Primate symphysis seems to have diverged relatively early from the typical Eutherian form.

4. In spite of very marked differences in type of symphysis there is observed throughout the Mammalia a definite and orderly type of symphysial metamorphosis which corresponds in its broad features with that already described for Man.

5. Certain easily distinguished subdivisions of the life span are common to all Eutheria, and by the use of these it is found that the age relationships of the various phases of symphysial metamorphosis can be indicated.

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PLATE I.

FIG. 1. Ornithorhynchus anatinus B 174. Twice nat. size. Note reptilian plate-like pelvis; subequal participation of both ischium and pubis in the symphysis; absence of any ossification representing the median bar; small epiphysis ossified but not yet united on ischial tuber.

FIG. 2. Echidna aculeata B 175. Nat. size. Complete ossification at the symphysis has taken place; a well-marked median crest is formed. This specimen and the last are in second life period.

FIG. 3. Petaurus breviceps B 187. Four times nat. size. Note median bar expanding above and below into nodules.

FIG. 4. Phascolomys tasmaniensis B 601. Nat. size. Note commencing ossification of lower nodule.

PLATE II.

FIG. 5. Dendrolagus inustus B 193. One half nat. size. The median disc penetrates backward between the symphysial faces. The median bar is simply its ventral and most constant part. Through the lower nodule it connects with the epiphysis for the ischial tuber.

FIG. 6. Petrogale xanthopus B 192. Three quarters nat. size. The ossification for the lower nodule is plainly seen; that for the upper nodule can only be seen from behind.

FIG. 7. Macropus bennetti. B 181. Note upper nodule with tongue of median disc extending downwards from it between the fusing symphysial faces.

FIG. 8. Phascolomys latifrons B 602. Nat. size. Complete fusion of pelvis at symphysis.

FIG. 9. Tupaia tana B 211. Twice nat. size. Compare the median bar with that in Petaurus Fig. 3.

FIG. 10. Arctomys monax B 127. Twice nat. size. Outer aspect of left side: deep aspect of right side. Note that the symphysial face is entirely upon pubis.

PLATE III.

FIG. 11. Trichys guentheri B 264. Five times nat. size. Note the completion of symphysial face by epiphysial continuation: no vestige of lower nodule. Bevelling of ventral margin preparatory to building of median bar.

FIG. 12. Dolichotis patachonica B 267. One and a half times nat. size. Note completion of symphysial face in "epiphysial" manner as in Trichys.

PLATE IV.

FIG. 13. Odocoileus virginianus B 634. Nat. size. Female. Note typical female appearance of symphysial face.

FIG. 14. Odocoileus virginianus B 649. Nat. size. Male. Note typical male appearance of symphysial face.

FIG. 15. Muntiacus muntjac vaginalis B 607. One half nat. size. Male. Note lower nodule as seen from behind.

FIG. 16. Odocoileus virginianus B 633. One half nat. size. Female. Note median bar (pencil) continuous below through lower nodule with epiphysis of ischium. Upper nodule does not develop.

FIG. 17. Felis tigris B 611. One half nat. size. Female. Note formation of ventral bar.

FIG. 18. Felis leo B 334. Female. Nat. size. Note ischio-pubic symphysial face.

FIG. 19. Felis leo B 173. Female. One half nat. size. Note secondary changes following upon "rim" formation in uncompleted upper extremity. Distinguish carefully from B 611, Fig. 17.

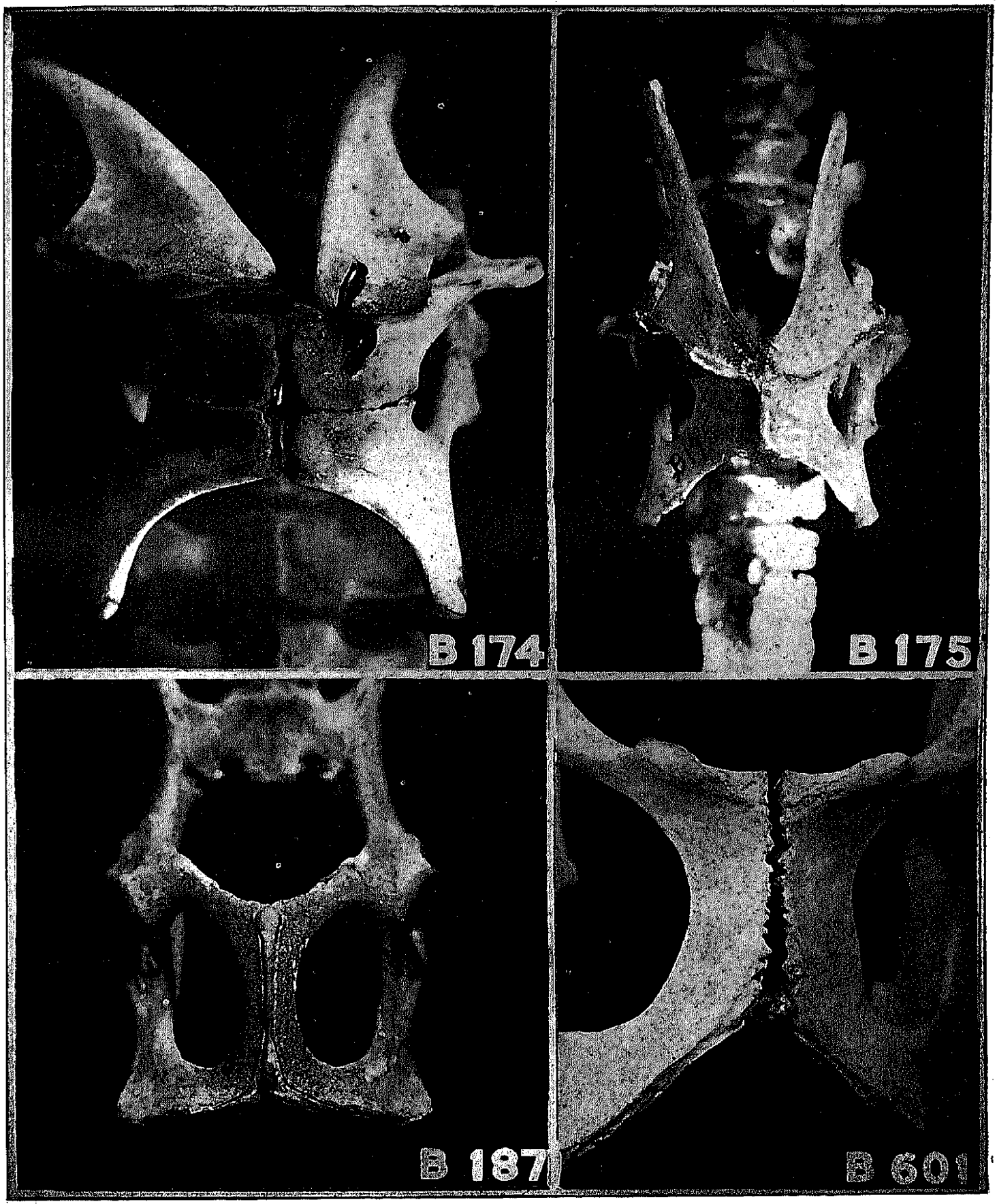

PLATE I

Upper row, Figs. 1, 2.
Lower row, Figs. 3, 4.

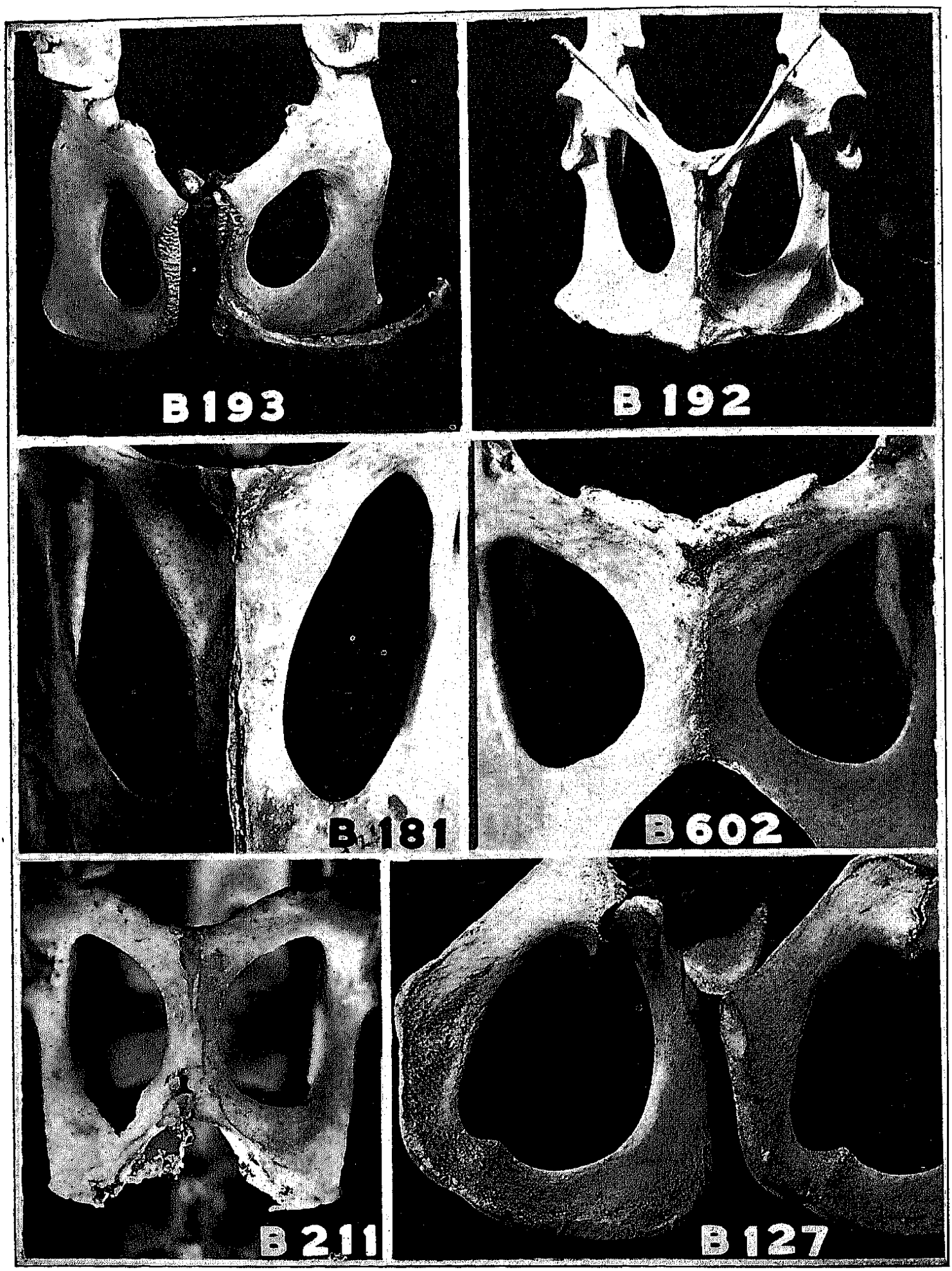

PLATE II

Top row, Figs. 5, 6.
Middle row, Figs. 7, 8.
Lowest row, Figs. 9, 10.

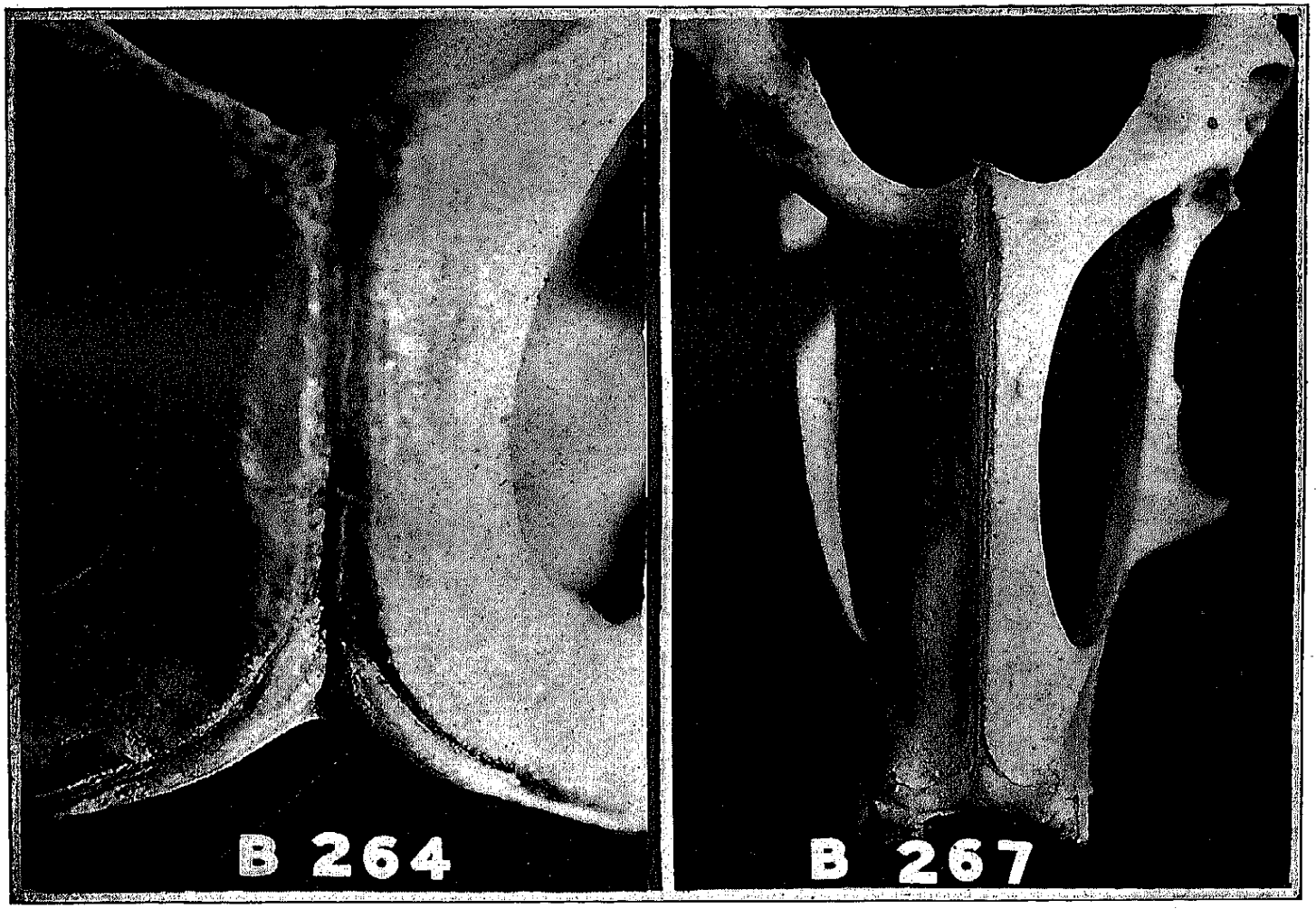

PLATE III

Figs. 11 (left), 12 (right).

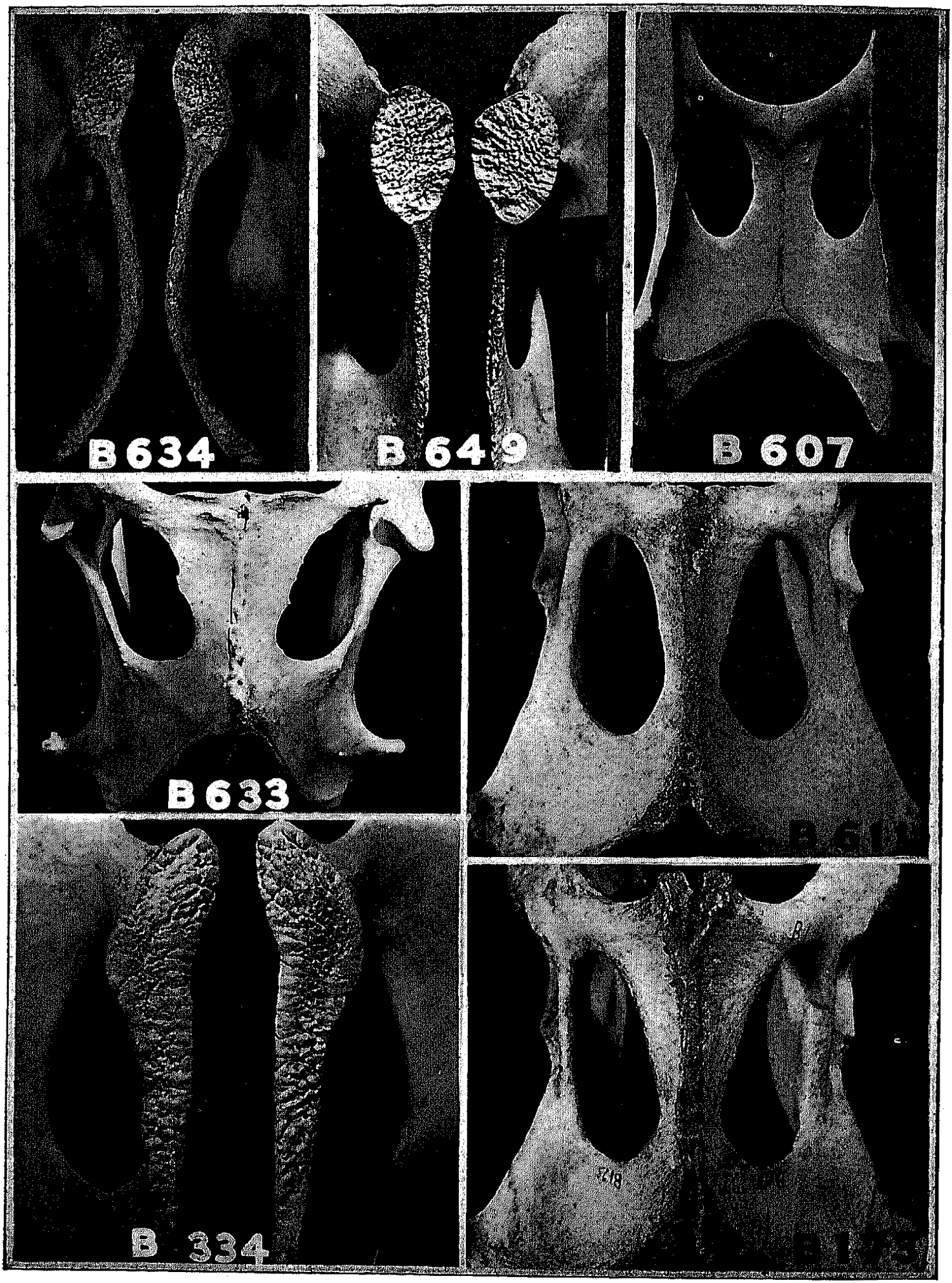

PLATE IV

Top row, Figs. 13, 14, 15.
Middle row, Figs. 16, 17.
Lowest row, Figs. 18, 19.

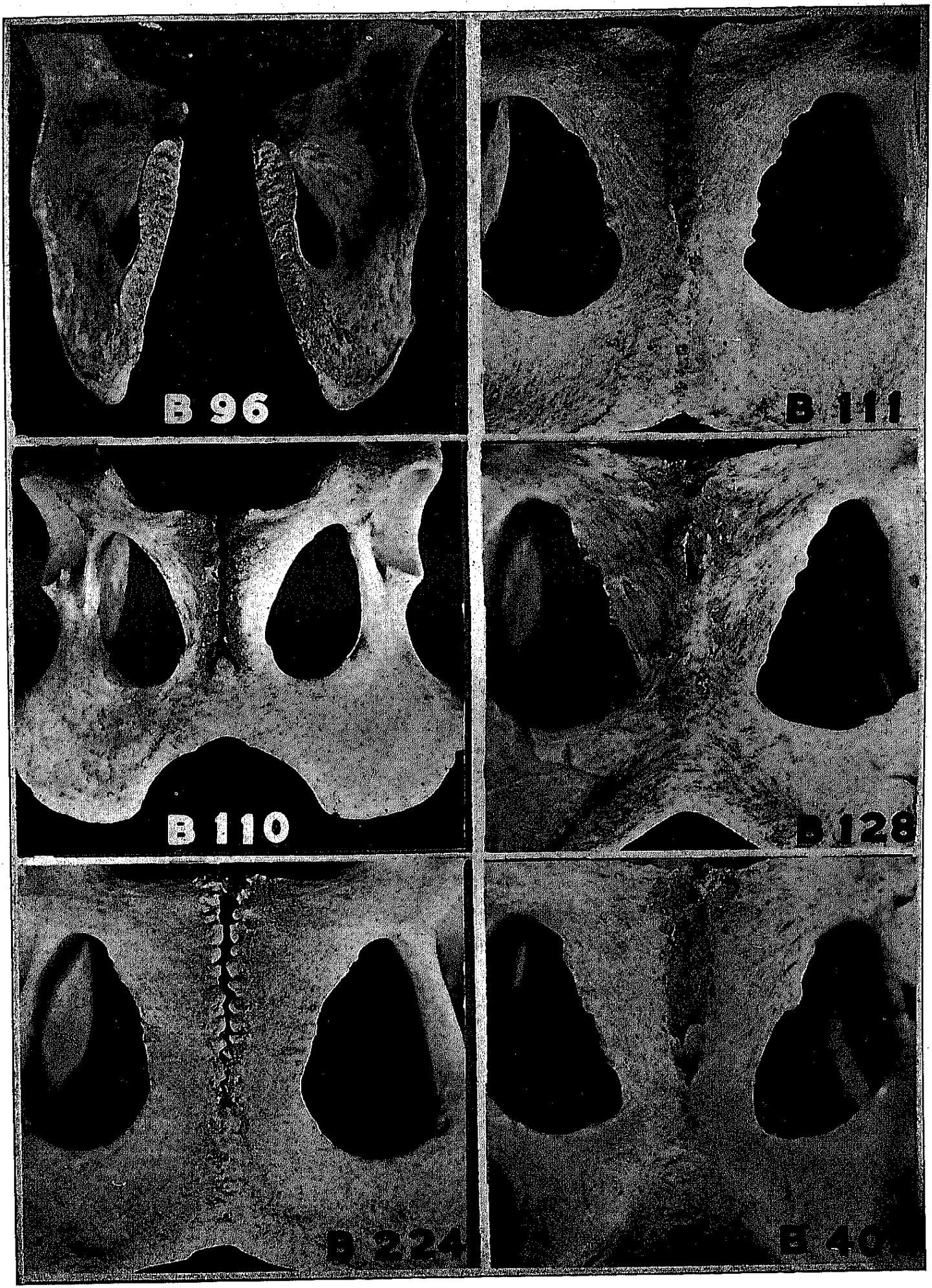

PLATE V

Top row, Figs. 20, 21.
Middle row, Figs. 22, 23.
Lowest row, Figs. 24, 25.

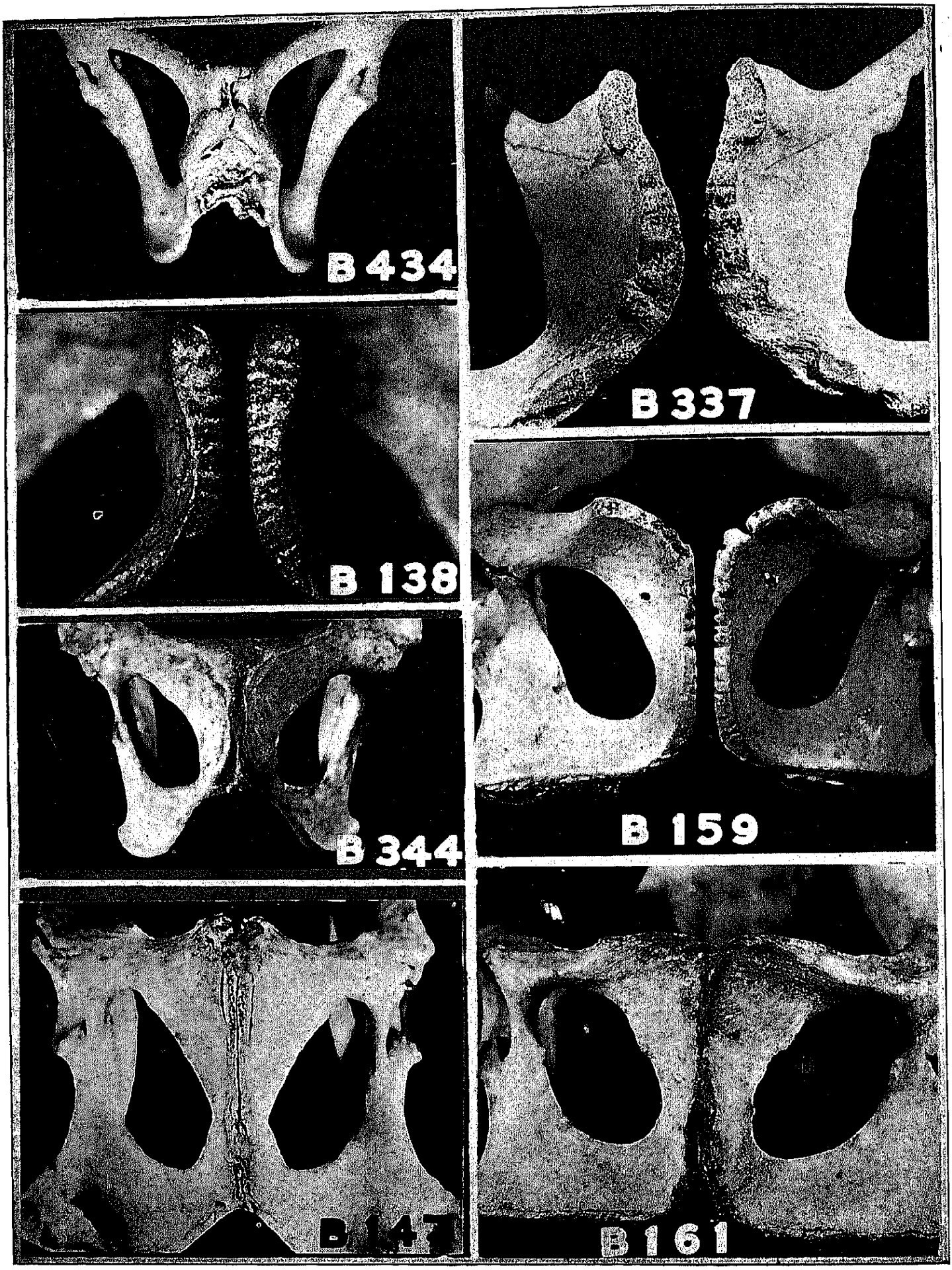

PLATE VI

Uppermost row, Figs. 26, 27.
Second row, Fig. 28.
Third row, Figs. 29, 30.
Lowest row, Figs. 31, 32.

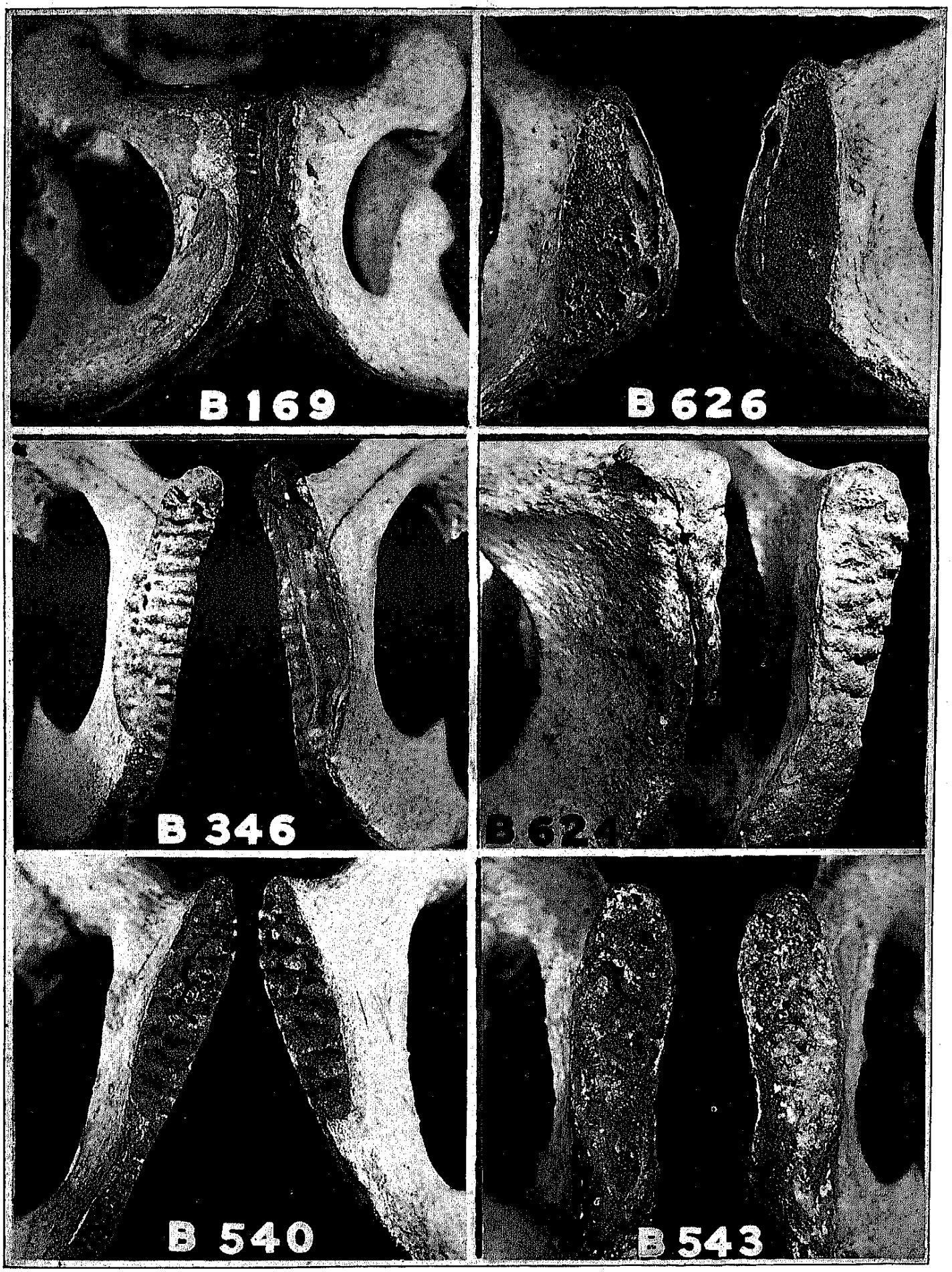

PLATE VII

Top row, Figs. 33, 34.
Middle row, Figs. 35, 36.
Lowest row, Figs. 37, 38.

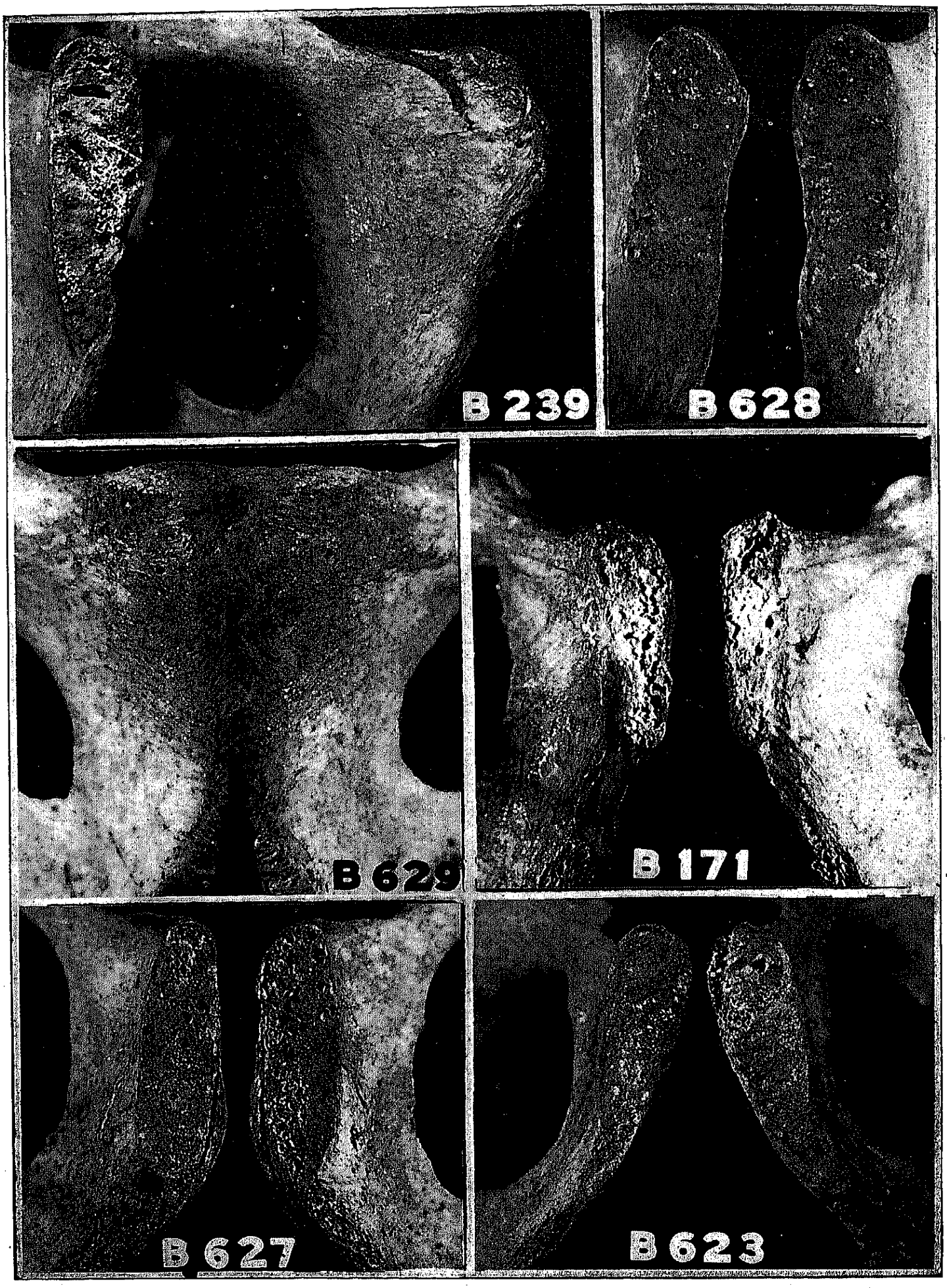

PLATE VIII

Top row, Figs. 39, 40.
Middle row, Figs. 41, 42.
Lowest row, Figs. 43, 44.

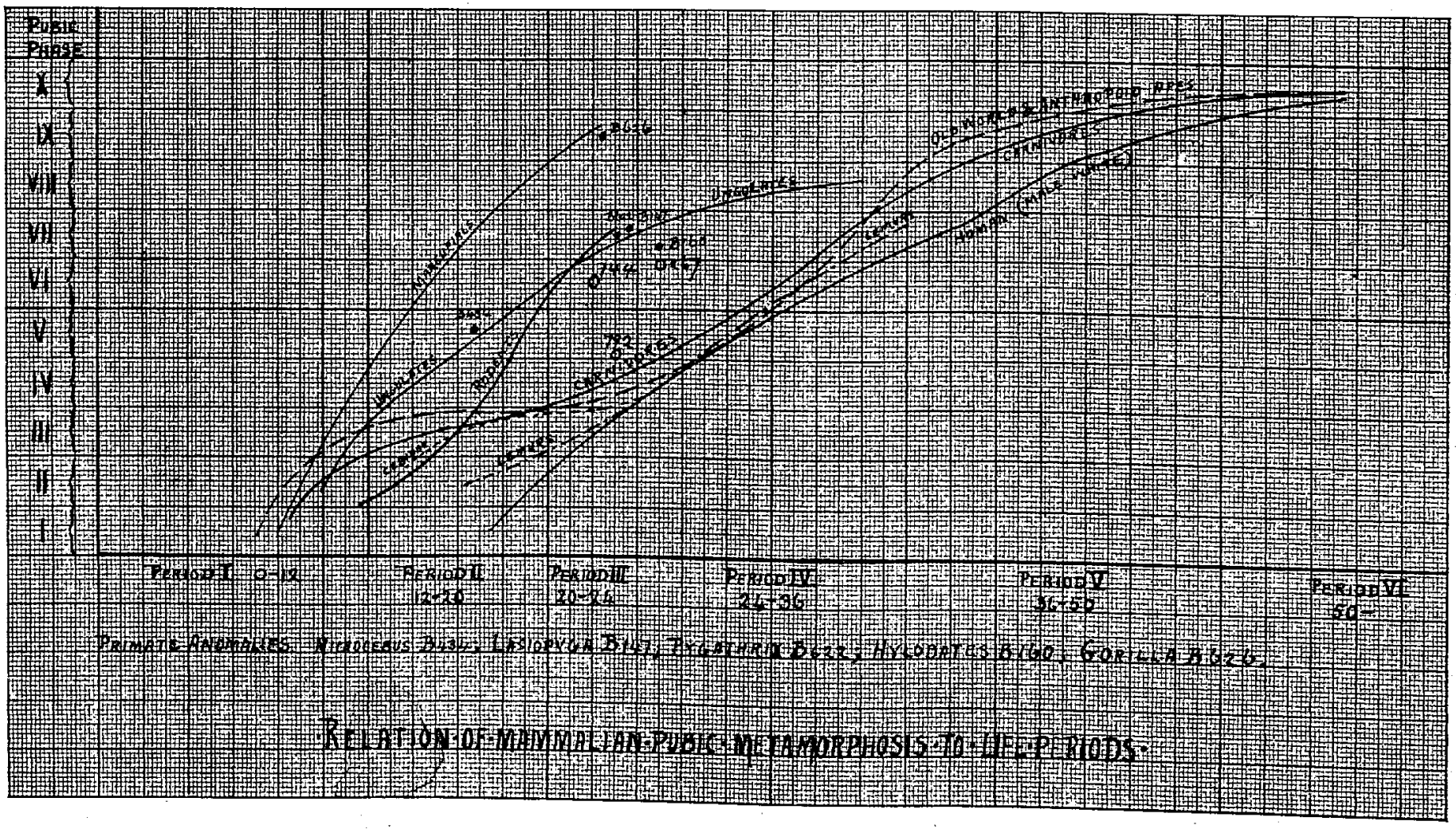
PUBIC PHASE
X
IX
VIII
VII
VI
V
IV
III
II
I
PERIOD I. 0-12
PERIOD II 12-20
PERIOD III 20-24
PERIOD IV 24-36
PERIOD V 36-50
PERIOD VI 50-
PRIMATE ANOMALIES: NYCTICEBUS BIRU; LEPILEMUR BIRU; TYLOCERUS BEZE; HYLOBATES BIGO; GORILLA BIZO.
RELATION OF MAMMALIAN PUBIC METAMORPHOSIS TO LIFE PERIODS.

FIG. 45

PLATE V.

FIG. 20. Canis familiaris B 96. Nat. size. Note ischio-pubic symphysis.
FIG. 21. Canis familiaris B 111. Nat. size. Fusion now involving pubis.
FIG. 22. Canis familiaris B 110. Nat. size. Note fused lower nodule. The ischia do not actually fuse together but are united through this nodule.
FIG. 23. Canis familiaris B 128. Nat. size. Completion of fusion. Note lack of union upper extremity and junction of upper and middle thirds of ventral margin.
FIG. 24. Canis familiaris B 224. Nat. size. Ischia and lower nodule completely fused: pubic portions not yet fused.
FIG. 25. Canis familiaris B 403. Nat. size. Secondary senile breaking down of ventral area.

PLATE VI.

FIG. 26. Microcebus murinus B 434. Five times nat. size. Note bilateral upper and lower nodules not yet fused.
FIG. 27. Pithecus nemestrinus B 337. Nat. size. Note distinction between true symphysial face and "extension" which is a secondary approximation of ischia.
FIG. 28. Lemur sp. B 138. Three times nat. size. Typical pubic symphysial face in phase II.
FIG. 29. Lemur variegatus B 344. Nat. size. Note large upper and smaller lower nodules already fused. Ventral margin forming. No fusion as yet between the two sides of the pelvis.
FIG. 30. Hylobates hoolock B 159. Nat. size. Phase II. Compare this with Fig. 29 and note area afterward occupied by upper nodule. Note approximation of ischia.
FIG. 31. Lasiopyga mona B 147. Nat. size. Phase VII. Fusion of ischia by secondary approximation.
FIG. 32. Hylobates concolor B 161. Nat. size. Phase VII+. Note approximation of ischia.

PLATE VIII.

FIG. 33. Gorilla sp. B 169. Nat. size. Quite young animal. Symphysial ridges and furrows. Phase I.
FIG. 34. Gorilla sp. B 626. Nat. size. Female: aberrant.
FIG. 35. Pan sp. B. 346. Nat. size. Phase III.
FIG. 36. Gorilla sp. B 624. Nat. size. Phase VI. Note median bar with no expanded lower nodule.
FIG. 37. Pan sp. B 540. Nat. size. Phase III. Note "extension" of symphysial face along ramus.
FIG. 38. Pan sp. B 543. Nat. size. Note completion of symphysial outline without intervention of median bar.

PLATE VIII.

FIG. 39. Gorilla sp. B 239. Nat. size. Commencing fusion of two pelvic halves broken in maceration. Left shown in face: right in ventral aspect.

FIG. 40. Pan sp. B 628. Nat. size. Typical phase VIII. No fusion.
FIG. 41. Pan sp. B 629. Nat. size. Typical phase VII+. with fusion. Contrast Fig. 40.
FIG. 42. Pan sp. B 171. Nat. size. Typical phase X. No fusion.
FIG. 43. Gorilla sp. B 627. Nat. size. Phase VIII supervening. Note large ridge (Cleland) for M. gracilis.
FIG. 44. Pongo pygmaeus B 623. Nat. size. Typical phase VI. No fusion.
FIG. 45. Graph of relation of pubic metamorphosis to age. (See text, especially p. 398.)