THE EXTENT TO WHICH THE POSTERIOR SEGMENTS OF THE BODY HAVE BEEN TRANSMUTED AND SUPPRESSED IN THE EVOLUTION OF MAN AND ALLIED PRIMATES.

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IN this paper the author proposes to deal with a section of a mass of evidence he has collected for a more accurate determination of the inter-relationships of the anthropoids, and of the kinship of man to that group of Primates. The data given here deal with the suppression of caudal segments, the transmutation of sacral to caudal, lumbar to sacral, and dorsal to lumbar segments, which have occurred in the bodies of that group of Primates of which man and the anthropoids are the living representatives. The evidence is sufficient to show that in the process of the evolution of this group of animals there has been no addition or suppression of segments in either the dorsal, lumbar, or sacral regions of the body; it is only at the distal end of the caudal series that suppression or addition may take place. Further, it will be shown that the transmutation of a body segment, in the evolution of a species, takes place, not by a bound, but by the gradual addition of minute variations.

That the bearing of the evidence of this section on the problem of the origin of the Higher Primates may be quickly grasped, it is necessary to state the working hypothesis which appears to be justified by the whole evidence at the disposal of the author. In the first place, he regards the Primates as divided into two very distinct groups—those which carry the axis of the body in a horizontal position—the *Pronograde Primates*, including the cynomorphous apes of the Eastern and Western hemispheres; and those which carry the axis of the body in an upright position —the *Orthograde Primates*, into which group fall the gibbon,

orang, chimpanzee, gorilla, and man.* The pronograde primate is certainly the earlier type; from it the orthograde was evolved, probably near the commencement of the Miocene Period. The earliest type of the orthograde primate of which we have any knowledge is the gibbon; from the Hylobatian (gibbon) type of orthograde primate have sprung what may be named—for temporary purposes—the *giant primates*, of which type the orang, the chimpanzee, gorilla, and man are the present-day representatives. This type was certainly gigantic, compared to its predecessors. The earliest giant-form we know is Dryopithecus, a Miocene anthropoid.

It will be thus seen that three well marked stages are recognised in the evolution of the highest primates—the pronograde stage, the orthograde stage, and finally, the giant stage. In the evolution of the human stock from that of the arboreal giant primates, a fourth stage must be recognised whereby man, by what means we know not, became adapted to plantigrade progression. The process of transmutation of the pre-sacral segments and suppression of the caudal began with the change from the horizontal to the upright posture during the evolution of the orthograde type from the pronograde. In all present-day pronograde apes—and we may safely suppose the same to hold true of their Miocene ancestry—the segmental formula is nearly constant—26 pre-sacral, 3 sacral, and 6-50 caudal segments. In the gibbon there are 25 pre-sacral segments; in man, the gorilla, and chimpanzee, 24; and in the orang, 23. Evidently, on the assumption of the upright posture there was an abbreviation of the trunk by one segment, and in the evolution of the giant primates still another segment was cut off from the pre-sacral series.

1. *The total number of Segments as determined by the number of vertebræ.*—The first point which required investigation was the total number of segments found in the various genera of living

* It is now generally recognised that the anthropoids, in their *natural habitat*, carry their bodies in an upright position, *i.e.* are orthograde. The misconception of the older naturalists sprang from their regarding the anthropoids as ground-walkers; for this method of progression they are as little adapted as seals or sea-lions. Instead of the terms *pronograde* and *orthograde*, my friend Mr P. Duncan, now Financial Secretary of the Transvaal, suggested Pronorachitial and Orthorachitial, but I have not used the terms.

Higher Primates, in order that data might be obtained to give a clue to the number of posterior segments which had been suppressed. The number of vertebræ was accepted as an index of the number of segments. In the following table (Table I.*) are given the results of this investigation.

TABLE I.

		Total Number of Vertebræ.								
		29.	30.	31.	32.	33.	34.	35.	36.	
	Specimens.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Average.
Orang . .	30	3·5	20	60	16·5	...	...	...	...	30·8
Gorilla . .	15	6·4	20	33	26·4	13·2	...	...	...	31·2
Chimpanzee	31	9·5	38·4	19	22	6·4	3·2	...	...	31·5
Man . . . (Paterson)	36	...	...	...	5·5	72·2	20	2·7	...	33·3
Man . . . (Bardeen)	104	...	...	...	5·8	85·5	8·5	...	...	33
Gibbon . .	51	...	...	14	32	24	12	12	6	33
Macacus,	...	...	...	...	...	...	...	...	...	33–49
Cynocephalus	...	...	...	...	...	...	...	...	...	36–44
Semnopithecus	...	...	...	...	...	...	...	...	...	58–60
Ateles	...	...	...	...	...	...	...	...	...	60–62
Cebus	...	...	...	...	...	...	...	...	...	54

From Table I. it will be seen (1) that within each genus of the orthograde primates there is a high degree of individual variation: orangs are found with only 29 vertebræ and gibbons occur with 36; between those extremes the vertebral formulæ of the gorilla, chimpanzee, and man form intermediate series; (2) that the process of suppression has affected the segments of the orang most and the gibbon least; (3) man has retained a larger number than any of the other giant primates, because, with the assumption of plantigrade progression, the caudal vertebræ assumed a new rôle in supporting the perineum. The extent of individual variation is evidence of the instability of the structure of the Higher Primates.

* The data of this and the following tables have been obtained from three sources —(1) from publications by many authors; (2) from personal dissections; (3) from the material in the museums of London. A full list of papers dealing with the Anatomy of the Primates was published by the author in 1896 (see "An Introduction to the Study of the Anthropoid Apes," *Natural Science*, 1896; also published separately). A list of subsequent literature from which data have been obtained is given at the end of this article.

The number of segments in a typical pronograde ape, such as the American Cebus or Asiatic Semnopithecus, is from 54 to 60 segments. The primitive orthograde stock arose probably from a pronograde ancestry with a corresponding number of segments; but, arguing from the condition seen in the genera Macacus and Cynocephalus, it is very possible that the caudal vertebræ were already largely suppressed before the orthograde posture was assumed. At least, the presence of a tail is incompatible with the orthograde posture. The number of vertebral segments in the *primitive orthograde stock* was probably about 36, the largest number that occurs in the gibbon—the nearest living representative of that stock.

With the assumption of the upright posture, the flexor and depressor muscles of the tail become modified to form a muscular pelvic floor. The tail of pronograde apes, even when only the four or five basal vertebræ remain, plays the part of a perineal shutter. The caudal vertebræ are amorphous and practically functionless in orthograde apes.

2. *The total number of Segmental Nerves, compared with the total number of vertebræ.*

A forward transmutation of a vertebra is usually accompanied by a corresponding transformation of every element of the body segment to which it belongs. The last lumbar vertebra, for instance, may take on, partly or wholly, the characters of a first sacral; the nerves, the arteries, the muscles of that segment usually undergo a corresponding movement to a corresponding extent. This correlation does not hold good for all the individual variations found in the human body, but it does hold true for the majority of such instances, as may be seen from the observations of Bardeen. When, however, different genera of primates are dealt with, a very close correlationship will be found between all the elements of a body segment. This will be seen in the correlation between the total number of vertebræ and spinal nerves in the various members of the Higher Primates (see Table II.).

TABLE II.

	Orang.	Gorilla.	Chimp.	Man.	Gibbon.	Prono-grade Apes.
The average number of vertebræ, . .	30·8	31·2	31·5	33·3	33	55
The average number of spinal nerves, .	28	29	30	31	31	33

In the evolution of the orthograde primates, the segmental nerves have undergone a forward transmutation nearly equal to

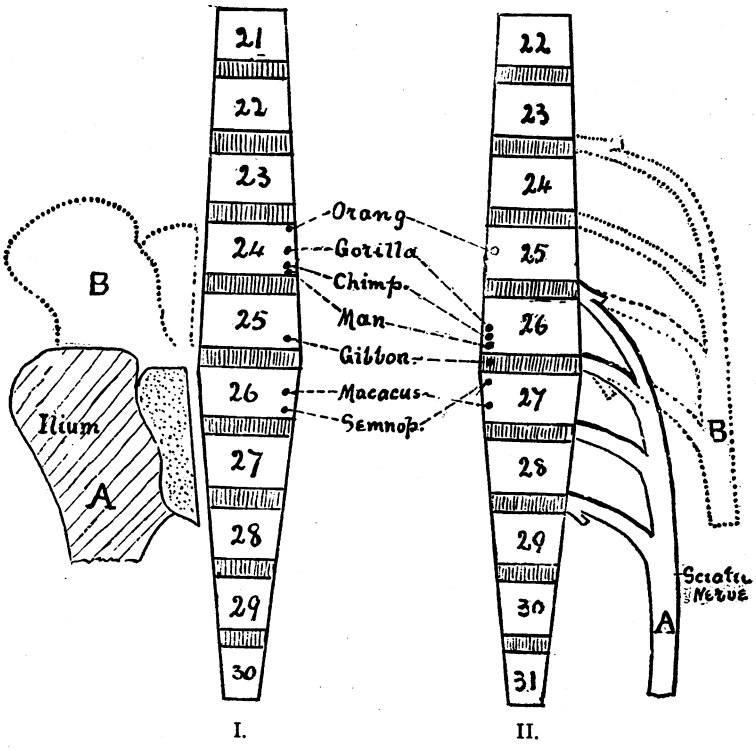

FIG. 1.—Diagram to show (I.) the point in the vertebral column at which sacralisation of the vertebræ commences in various genera of the Higher Primates, and (II.) the central point of emergence of the great sciatic nerve in the same genera.

that of the *body* segments (see fig. 3). On the other hand, sup-

pression of caudal vertebræ has little influence on the total number of nerves; pronograde forms have only two or three pairs more than the gibbon, the most primitive of the orthograde primates. In Ateles, owing to the specialisation of its tail as an organ of prehension, 40 of the segments may carry spinal nerves, but in the more common pronograde apes the number varies from 32 to 34.

3. *The number of Pre-sacral Segments.*—A certain number of body segments are modified to give attachment to the limbs. In pronograde apes the sacral segments are almost constant in number and position, the vertebra of the 27th segment forming the first sacral. With the assumption of the orthograde posture and the shortening of the loins entailed by that change (see fig. 4) there was evidently a transmutation forwards of a whole segment, the last lumbar (26th) becoming wholly sacral in character. The vertebra of the 26th segment became the first sacral. At least in the gibbon, which may be accepted as a representative of the primitive orthograde stock, seeing how closely the present-day animal resembles its Miocene ancestor, the 26th vertebra forms the first sacral. In the evolution of the giant primates there was still a further transmutation forward of one segment, the 25th becoming the 1st sacral. In the orang, for reasons which will be given later, the transmutation has reached the furthest point forward, sacralisation commencing at the proximal border of the 24th segment. The data on which these inferences are founded is given in Table III. In that table it will be seen that the point at which sacral transformation occurs in the segmental series is variable in each genus of the orthograde primates. The genera dealt with in Table III. show sacral transformation setting at every segment between the 23rd and 28th, the variations of one genus overlapping those of the next.

TABLE III.

		Vertebra forming the 1st sacral.						
		23rd.	24th.	25th.	26th.	27th.	28th.	
		Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Average
Orangs . . .	46 specimens.	5·4	77	17·5	...	...	...	23·1
Gorillas . . .	27 ,,	7·4	37	55·6	...	...	...	23·5
Chimpanzees .	38 ,,	2·6	19·7	55·2	22·3	...	...	23·9
Men	358* ,,	...	3	92	5	...	...	24·02
,, ...	104† ,,	...	8·5	85	7·5	...	...	23·9
Gibbons . .	59 ,,	...	...	15·2	78	6·8	...	24·9
Ateles . . .	6 ,,	...	...	10	80	10	...	25
Macacus . .	19 ,,	...	...	...	45	53	2·8	25·6
Cynocephalus .	8 ,,	...	...	...	37·5	50	12	25·7
Semnopithecus	15 ,,	...	...	...	4	96	...	25·9
Cebus . . .	10 ,,	...	...	...	10	50	40	26·3

For the purpose of comparing the extent to which the hinder lumbar segments have been affected by the process of sacral transformation in each genus, it is necessary to take the average point in the segment-series at which sacral transformation commences. That point can be determined only to an approximate degree. In the orang the point at which sacral transformation commences in the average animal is a little below the proximal border of the 24th segment (see fig. 1, A); sacralisation begins nearly half a segment further back in the average gorilla; in the chimpanzee and man the change commences near the distal border of the same segment. In the negro, sacralisation commences nearly one-third of a segment further back than in white races. In the gibbon, sacral transformation begins near the distal border of the 25th segment, rather more than a segment further back than in the giant primates. In Semnopithecus, probably the best representative now living of the early Miocene pronograde apes, sacral modification starts near the distal border of the 27th segment—one segment further back than in the gibbon.

Why should there have been a forward sacral transmutation

* These statistics are obtained from various authors, including Paterson, Rosenberg, Tenchini, and Papillaut.

† Bardeen's statistics. More than half of his observations were made on negroes in whom the limbs are attached rather more than a third of a segment more posteriorly than in white men.

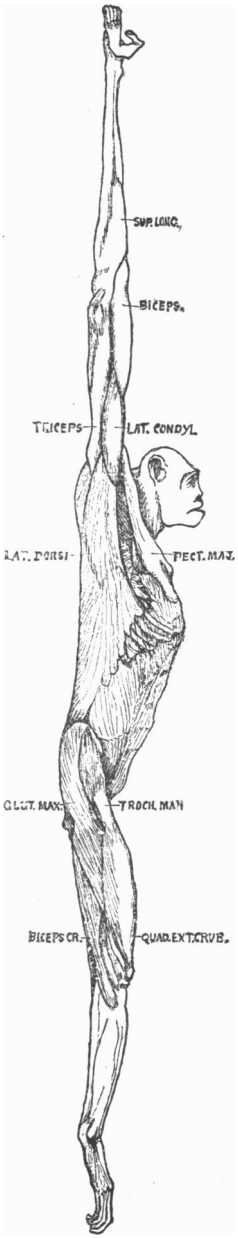

FIG. 2.—Diagram of a Gibbon (*Hylobates lar*), suspended by its arm to show the adaptation of the muscles and trunk to its brachiating mode of progression —(from a photograph).

of the body segments in the evolution of the orthograde and giant primates? The reason is to be sought for in their adaptation to a new form of locomotion. The long rod-like lumbar region of the jumping and climbing pronograde ape becomes unnecessary for an orthograde form like the gibbon, supported more from its arms than on its legs (see fig. 2). In the evolution of the giant primates the pelvis became still more closely knitted to the body, and the lumbar region correspondingly shortened (fig. 4). On the evidence at present at his disposal, the author believes that the evolution of the primitive orthograde primates early in the Miocene Period was attended by the addition of a lumbar segment to the sacral region; with the evolution of the giant primates later in the Miocene, still another lumbar segment was added to the sacral. It was probably at the stage just mentioned at which the human stock broke away from the common giant primate stock. The assumption of plantigrade progression necessitated a longer loin (fig. 4), which was evidently obtained by a suppression of one pair, perhaps two, of ribs. The transformation of a third lumbar to a sacral segment in the orang is probably a comparatively late acquisition following on its brachiating habits of progression. While the upper extremities of the orang are enormously developed, the lower limbs are comparatively small and show many traits of degeneration. The upper half of its body is developed at the expense of the lower half.

4. *A forward progression in the origin of the great Sciatic Nerve.*—With the transmutation of the distal lumbar vertebræ into sacral there was a movement forward, although not to a corresponding extent, of the points at which the nerve fibres which form the great sciatic nerve make their exit (fig. 1 B). The segmental nerves which contribute to the formation of the great sciatic nerves in various genera of primates are shown in Table IV.

TABLE IV.

Spinal Nerves .	Specimens.	23rd.	24th.	25th.	26th.	27th.	28th.	29th.	Central Point of Origin.
Orang . . .	5	5	5	5	5	...	...	...	24·5
Gorillas . . .	5	...	4	5	5	5	1	...	25·7
Chimpanzees .	6	...	4	6	6	6	2	...	25·8
Man (Eisler)	126	2	107	126	126	124	22	...	25·6
,, (Bardeen)	246	11	223	246	246	245	157	35	25·9
Gibbon . . .	9	...	4	9	9	9	5	...	26·
Macacus . . .	10	...	...	5	10	10	10	...	26·7
Semnopithecus .	18	...	...	13	18	18	3	...	26·2

In order to compare one genus with another, and the degree of nerve and vertebral migration, it is necessary to fix a point which marks the centre at which the nerve fibres contributing to the great sciatic make their exit. In the orang, in which the sciatic nerve arises from the 23rd to the 26th, the central point of its origin lies near the mid point of the 25th segment (see fig. 1 B); the central points of exit for the gorilla, chimpanzee, and man lie on the 26th vertebra, in order from above downwards; on the proximal border of the 27th in the gibbon. Eisler's statistics place the central point for man above those of the gorilla and chimpanzee; Bardeen's below them, probably because his observations were made on the negro as well as the white man. The central points of origin of the sciatic nerve in Macacus and Semnopithecus, as shown in fig. 1 B, are situated on the 28th segment.

The observations which have been made on the anthropoids are too limited in number to afford more than a rough approximation to the truth; but it is evident, considering the Higher Primates as a group, that a transmutation of the nerve elements of a segment has accompanied the sacralisation of the vertebræ (compare fig. 1 A and fig. 1 B). In pronograde apes the central point of origin of the great sciatic nerve and the point at which sacralisation of the vertebræ commences is situated in the 27th segment; in the gibbon these two points are situated a segment further forwards; but in the giant primates, sacralisation of the vertebræ starts a segment further forwards than the central point of origin of the sciatic nerve.

It will be seen afterwards that the development of the costal

series influences the position of the origin of the sciatic nerve; in Semnopithecus and the orang, in which the origin of the sciatic nerve is more proximal than one would expect, the costal series have been abbreviated; in the gorilla and chimpanzee, the costal series reach their full number, and in these animals the central point of origin of the great sciatic nerve is more distal than one would expect. In man, the origin of the great sciatic nerve is also lower than is to be expected, and yet in him the costal series has been reduced, and therefore, if the explanation offered for the others is right, in him the origin of the sciatic nerve ought to be high. The low position in man is probably owing to the great development of his lower extremities.

It is evident that if such a transmutation of the hinder segments of the body has taken place during the evolution of the giant primates, that the segmental distribution of the cutaneous nerves on the lower limbs must have been disturbed. In pronograde apes, as we know from the classical researches of Sherrington, the segmental distribution of the cutaneous nerves is regular and symmetrical in the lower limbs, but such symmetry and order have not been found in the segmental distribution of the nerves in the lower limbs of man. The discrepancy is probably due to a disturbance which occurred in the forward transmutation dealt with here. It is probable that the segmental distribution of cutaneous nerves is not exactly alike in the lower limbs of any two human bodies, and hence the discrepancy in the results of different observers.

5. *The number of Sacral Segments.*—Since it is the 27th, 28th and 29th body segments which undergo sacral modifications in the typical pronograde apes of the Western and Eastern hemispheres, there can be little doubt that these were the sacral segments in the pronograde stock from which the orthograde was evolved. With the assumption of the upright posture in the early orthograde primates, of which the gibbon is the best living representative, the 26th segment underwent sacral modifications; with the evolution of the giant primates, still another, the 25th, was added to the sacral segments; and still later, in the stock of the orang, the 24th. Thus in the orang there ought to be found six sacral vertebræ; in the gorilla, chimpanzee, and man five, in the gibbon four, in pronograde apes three.

The annexed table (Table V.) will show how far this expectation is well founded.

TABLE V.

Number of Sacral Vertebræ.	Specimens.	2.	3.	4.	5.	6.	7.	8.	Average.
Orang . . .	37	...	...	12	24	1	...	...	4·7
Gorilla . . .	24	...	3	1	13	5	1	1	5·1
Chimpanzee .	31	...	2	3	13	12	1	...	5·2
Man (Paterson)	100	...	...	2·6	61·8	34·3	1·13	...	5·3
,, (Bardeen)	100	...	...	5·7	86·6	7·7	...	...	5·02
Gibbon . . .	68	...	12	26	26	4	...	...	4·3
Ateles	3	...	1	2	...	...	...	...	3·6
Semnopithecus .	...	rare	com.	...	...	...	...	...	−3
Macacus . . .	...	...	com.	rare	...	...	...	...	+3

On the average, the number of sacral vertebræ answers to the number expected. In the gibbon there are 4, in man, the gorilla and chimpanzee 5, but in the orang there are less than 5, while 6 is the number to be expected. The reduction in the number of the sacral vertebræ in the orang is due, as will be shown in the next paragraph, to a caudal transformation of the posterior sacral segments. In pronograde apes only two vertebræ articulate with the ilium, in orthograde there are three. The gibbon, gorilla and chimpanzee show a greater instability in the number of sacral vertebræ than man, because in them it plays a less defined and less important part in their locomotion.

6. *The caudal transmutation of the distal Sacral Vertebræ.*—While the distal lumbar segments were undergoing a sacral transformation, there was only a slight movement in the direction of turning distal sacral segments into caudal. In man and the gibbon the first caudal vertebræ is the 30th, and this seems to be the primitive form, for in all the typical pronograde apes the 30th is the first vertebra of the tail. In the orang and gorilla, in which the forward transmutation of segments is most marked, the last sacral (29th segment) has undergone a caudal modification. As may be seen from Table VI., in which the serial number of the vertebra forming the first caudal or coccygeal is given, the extent of individual variation is very great.

TABLE VI.

Vertebra forming the first caudal.	27th.	28th.	29th.	30th.	31st.	32nd.	
Specimens.							Average.
Orang . . . 15	...	3	10	2	...	...	−29
Gorilla . . . 18	2	4	4	7	1	...	+29
Chimpanzee . . 31	2	8	3	15	3	...	29·3
Man (Paterson) . 132	...	...	3	103	24	2	30·2
,, (Bardeen) . 104	...	...	6	89	9	...	30
Gibbon . . . 49	...	...	12	19	12	6	30·2

Occasionally in Macacus the 29th, and in Semnopithecus and Cebus the 31st vertebra forms the first caudal; but normally in all three genera, the 30th forms the first of the caudal series.

7. *The number of Caudal or Coccygeal Vertebræ.*—The distal sacral and all the caudal vertebræ of the anthropoids are frequently so vestigial in form that it is hard to say which is the first caudal, and how many the caudal vertebræ are in number. It is probably owing to this difficulty that there is a discrepancy in the statistics which are given relating to the orang. In that anthropoid the 24th is the first sacral vertebra; there were, on an average, less than 5 sacral vertebræ; therefore the first caudal ought to be the 28th and not 29th, as the statistics show. Table VI., too, is founded on a smaller number of animals than Tables III. and V. In the following table (Table VII.) the number of caudal vertebræ in each genus is given.

TABLE VII.

Number of Caudal Vertebræ.	2.	3.	4.	5.	6.	7.	
Specimens.							Average.
Orang . . . 20	4	12	2	2	...	...	3·1
Gorilla . . . 13	3	5	3	2	...	...	3·3
Chimpanzee . 32	5	12	5	7	3	...	3·7
Man 104	9	95		...	...	...	3·(?)
Gibbon . . . 54	6	18	22	5	1	2	3·7
Semnopithecus ...	...	...	...	...	...	...	30
Macacus	...	...	...	...	...	...	4–21
Cynocephalus	...	...	...	...	...	...	6–10

The most striking point relating to the caudal vertebræ of the anthropoids is their variability in number, and their amorphous

and vestigial character. In comparison with these, the human caudal vertebræ are steadfast in number and much better formed.

With the assumption of the upright posture in the primitive orthograde primates, the tail became a useless structure and underwent suppression. It was no longer required to play the part of a balancing rod or perineal shutter. It is not improbable that the process of caudal retrogression had set in long before the change in posture took place, for in many modern species of pronograde apes belonging to the Macaque and baboon genera, the typical number (30) of caudal segments is reduced to 4 or 6, but in such cases of reduction the vertebræ still retain all the characters of fully developed caudal vertebræ, still act as a perineal shutter, and in no way resemble the amorphous remnants of the caudal vertebræ in orthograde primates. With the change of posture there was a radical change in the formation of the pelvic floor.

The adaptation of the tail as a prehensile organ, which has led to many changes in the structure of South American apes, is probably to be regarded as a comparatively recent acquisition.

8. *The transmutation of Lumbar Segments as indicated by the origin of the anterior crural nerve.*—In the segmental origin of the anterior crural or femoral nerve, evidence is to be found of the degree to which the proximal lumbar segments have been affected in the general forward transmutation that set in with the assumption of the upright posture. The segmental nerves which contribute to the formation of the anterior crural in various groups of the Higher Primates is set forth in Table VIII.

TABLE VIII.

		Spinal Nerve.							Central Point of Origin.
		20.	21.	22.	23.	24.	25.	26.	
	Specimens.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	
Orang	9	1	7	9	9	1	...	...	22
Gorilla	6	...	1	5	6	6	1	...	23
Chimpanzee	11	...	3	9	11	10	2	...	23
Man (Bardeen)	246	2	90	246	246	246	37	...	22·8
Gibbon	11	...	...	1	10	11	6	...	23·8
Semnopithecus	10	...	...	3	6	10	7	...	23·8
Macacus	9	...	...	...	5	9	9	...	24·1

In fig. 3 is shown the central point of origin of the anterior crural nerve in each genus of the Higher Primates dealt with here, and it will be seen by comparing the origin of this nerve with that of the great sciatic that there is not a close correlation between the forward movements of those two nerves. The condition in Semnopithecus may be taken as typical of pronograde apes, and in it the central point of origin of the anterior crural nerve is situated near the distal border of the 24th vertebra. In the orang the origin of this nerve has moved forwards nearly two segments; in man, the gorilla and chimpanzee, one segment; but in the gibbon the pronograde origin is retained. It will be seen presently that the origin of the anterior crural nerve is correlated with the development of the costal series; with the retrogression of the distal ribs there is a forward movement in the origin of this nerve. The origin of the anterior crural is acted on by two influences: (1) the forward transmutation of lumbar to sacral segments, and (2) of the transformation of dorsal to lumbar.

9. *The origin of the Obturator Nerve.*—In the transmutation of lumbar segments the obturator nerve does not follow closely the migration of the anterior crural. In Table IX. are shown the various segmental nerves which contribute to the formation of the obturator.

TABLE IX.

	Specimens.		Spinal Nerves. 21.	22.	23.	24.	25.	26.	Central Point of Origin.
			Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	
Orang	8		2	7	8	...	...	...	22·3
Gorilla	6		...	5	6	6	1	...	23·2
Chimpanzee	4		1	3	4	3	...	...	22·8
Man	246	(Bardeen)	84	246	246	245	25	...	22·8
Gibbon	11		...	...	4	11	7	...	24·2
Semnopithecus	9		...	...	...	9	9	1	24·6
Macacus	8		...	...	1	7	8	4	24·7

In man the origin of the anterior crural nerve and obturator is practically the same, the central point of origin for both being the junction of the distal fifth with the proximal four-fifths of the 23rd vertebra. In pronograde apes, on the other hand, the

obturator nerve takes its origin at least half a vertebra behind

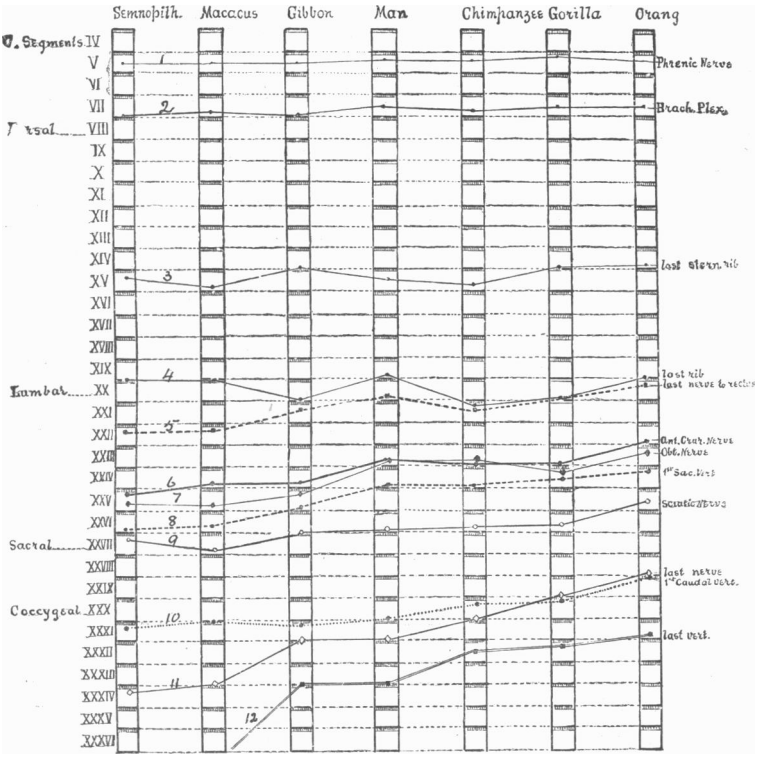

FIG. 3.—A composite diagram representing the vertebral columns, from the 4th to the 36th vertebræ, of various genera of Higher Primates. On each vertebral column, founded on the statistics given in the text, are represented the following points :—

(1) The central point of origin of the phrenic nerve.
(2) ,, ,, ,, brachial plexus.
(3) The segment carrying the last sternal rib.
(4) ,, ,, ,, rib.
(5) The point of origin of last nerve to rectus abdominis.
(6) The central point of origin of the anterior crural or femoral nerve
(7) The central point of origin of the obturator nerve.
(8) The point at which sacralisation of the vertebræ commences.
(9) The central point of origin of the great sciatic nerve.
(10) The point at which the vertebræ becomes caudal.
(11) The point of origin of last spinal nerve.
(12) The last vertebra.

that of the anterior crural ; in the gibbon, orang and gorilla the

origin of the obturator approaches, in the order named, the origin of the anterior crural; in the chimpanzee, the origin of the obturator appears to be slightly proximal to that of the anterior crural.

10. *The number of Rib-bearing Segments.*—Owing to the lack of evidence, it is a difficult matter to fix approximately the number of rib-bearing segments in the primitive stock of the orthograde primates. Even in typical living pronograde apes such as Semnopithecus and Colobus, there has been a suppression of at least one pair of ribs in the more recent periods of their evolution, so that in the matter of rib-bearing segments these no longer represent the pronograde stock which gave rise to the orthograde. From the evidence adduced in Table X., in which the last rib-bearing segment is given in most of the genera of the Higher Primates, it will be seen that the 8th to the 21st segments are costal-bearing, making 13 pairs of ribs.

TABLE X.

		Last Costal-bearing Segment.						
		17.	18.	19.	20.	21.	22.	
	Specimens.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Average.
Orang	31	...	4	87	9	...	...	19·02
Man	104 (Bardeen)	...	5·7	90*	3·8	...	...	18·9
Gorilla	29	...	...	10	84	6	...	19·96
Chimpanzee	35	...	...	...	83	17	...	20·1
Gibbon	33	...	...	9	82	9	...	20
Semnopithecus	31	...	3	94	3	...	...	19
Macacus	...	...	...	95	5	...	...	19·05
Cynocephalus	...	...	...	25	75	...	...	19·7
Ateles	...	...	...	...	...	100	...	21

Assuming that the 20th was the last costal-bearing segment in the primitive stock from which the various genera of primates dealt with here arose, it will be seen that this number has been approximately retained in the gorilla, chimpanzee and gibbon. In the pronograde apes of the Eastern hemisphere the number has been reduced, Cynocephalus suffering the least degree

* In 40 per cent. of these the 12th rib was less than two inches long, and therefore could scarcely be regarded as forming part of the thorax.

of suppression. It is probable that the number has been increased in Ateles, and there appears to be a tendency to increase in the chimpanzee. The fact that the diaphragm in all the genera of primates mentioned in the above tables has an attachment to the rib or costal process of the 20th segment, however vestigial that process may be, points to the fact that the 20th segment has always been, as far as the Higher Primates are concerned, the last of the respiratory segments.

It will be observed, too, that there is only a slight correlation between the forward progression of the sacral segments and the reduction of the distal costal processes. The orang, in which three lumbar have become sacral segments, has suffered reduction in only one costal segment. The reduction in the number of the costal segments in man, Semnopithecus and Macacus is due, not to any retrogression in their respiratory system, but to an elongation of the lumbar region of the spine rendered necessary in those forms by their manners of progression.

11. *Reduction in the number of Sternal Segments and Sternal Ribs.*—In the suppression of the distal costal segments there has been some reduction of the distal sternal segments, which may be indicated, as shown in Table XI., by the number of sternal ribs.

TABLE XI.

Last Sternal Rib.	6th.	7th.	8th.	9th.	10th.	
	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Average.
Orang	18	82	...	...	...	6·8
Man (white) . .	2	90	8	...	...	7·2
,, (negro) . .	...	70	30	...	...	7·3
Gorilla	5	85	10	...	...	7
Chimpanzee . .	...	54	46	...	...	7·4
Gibbon	8	78	14	...	...	7
Semnopithecus .	4	72	24	...	...	7·2
Macacus	...	12	88	...	...	7·8
Cynocephalus . .	...	...	60	40	...	8·4
Ateles	...	...	33	55	35	9

With some exceptions, the reduction in the number of sternal ribs corresponds in a minor degree with the sacral transmutation of the distal lumbar segments, and also with the reduction in the total number of costal-bearing segments. The sternal ribs

are fewest in the orang, in which the forward sacral transmutation has proceeded furthest; the gorilla follows next; the chimpanzee has a larger number of costal-bearing segments and sternal ribs than any of the other orthograde primates. The reduction in the number of sternal ribs in the gibbon has to be sought for in the peculiar development and use of the pectoral muscles (see fig. 2).

12. *Transmutation in the distal, cervical and proximal dorsal Segments.*—The proximal 18 segments of the body, compared with those situated more distally, have undergone a very slight degree of transmutation during the evolution of the various genera of primates. In all the extant genera, as was no doubt the case in the original stock of the primates, the 8th is the first rib-bearing segment. Occasionally in man, the gibbon and chimpanzee, the 7th cervical segment may take on partially or even wholly the characters of the 8th; very rarely indeed is there a backward transmutation when the 8th takes on the characters of the 7th. The extent of the transmutation in this region of the body may be measured by the central points of origin of (1) the phrenic nerve, (2) the brachial plexus; and although the data I have collected bearing on the segmental origin of those two relate to a comparatively small number of individuals, they are sufficient to show that, in the origin of the brachial plexus and phrenic nerve, there is not, as shown in fig. 3, half a segment of difference between the two most extreme forms. The central point of origin of the phrenic nerve is always at a point on the proximal half of the 5th segment, that of the brachial plexus on the distal half of the 7th.

Occasionally, too, there is a partial occipitalisation of the first (cervical) body segment, the atlas being incompletely separated from the occipital bone.

13. *The last Segmental Nerve of the belly wall.*—An examination of the ventral aspect of the body reveals the fact that the segmental abbreviation of the trunk has proceeded rather more slowly on the ventral than on the dorsal aspect. The data on which this statement is based is given in Table XII. There the last nerve supplying the rectus abdominis is given in groups of the Higher Primates.

TABLE XII.

Last Segmental Nerve to Rectus.	Specimens.	19th.	20th.	21st.	22nd.	23rd.	Average.
Orang	5	4	1	...	...	...	19·2
Gorilla	4	2	1	1	...	...	19·7
Man (Bardeen) .	267	44	214	9	...	...	19·8
Chimpanzee . .	7	...	5	2	...	...	20·3
Gibbon	11	...	7	3	1	...	20·4
Semnopithecus .	3	...	...	2	1	...	21·3
Macacus . . .	6	...	...	4	2	...	21·3
Cynocephalus .	...	...	...	...	...	...	22

14. *Abbreviation of other structures.*—In comparing the level at which certain viscera occur in the body, one must remember that most of the anthropoids dissected are young animals, and the position of their viscera is comparable, not with those of adult man, but with those of the child. The point of bifurcation of the trachea, the position of the arch of the aorta, and the level of the cricoid cartilage correspond in man and anthropoid. Alteration in position affects only viscera on a level with the distal lumbar segments. Thus the abdominal aorta bifurcates at the level of the 24th vertebra in pronograde apes, or even at a point situated more distally; at a level with the 23rd vertebra in the gorilla, chimpanzee, gibbon and man; and at the 22nd in the orang.

The spinal cord terminates at the 19th vertebra in the orang, 22nd in the *baby* gorilla, 20th in the chimpanzee, 21st in man, 22nd in the gibbon, 23rd in Macacus and Semnopithecus, and 24th in Ateles.

15. *A comparison of the proportions of the cervical, dorsal and lumbar regions of the spine.*—In fig. 4 are represented diagrammatically the relative lengths of the cervical, dorsal and lumbar regions of the spines in various genera of the Higher Primates. The diagram is founded on measurements made by Cunningham, the author, and other observers on several specimens of each genus. It will be seen at once that with the *sacralisation* of the distal lumbar segments there is also a reduction in the relative length of the lumbar region. In the orang, where the process has proceeded furthest, the lumbar region is shortest, measuring only 24 per cent. of the pre-sacral

part of the spine. The lumbar region is relatively longest in the pronograde apes. Man occupies a curious position. At birth the lumbar region is only 27 per cent. of the pre-sacral spine; but as the child learns to walk, the lumbar region elongates and becomes ultimately 32 per cent. of the spine, equal to that of the gibbon. Thus at birth the proportions of the regions of the human spine are those of an anthropoid. The short lumbar region of the orang, as already explained—and the explanation is

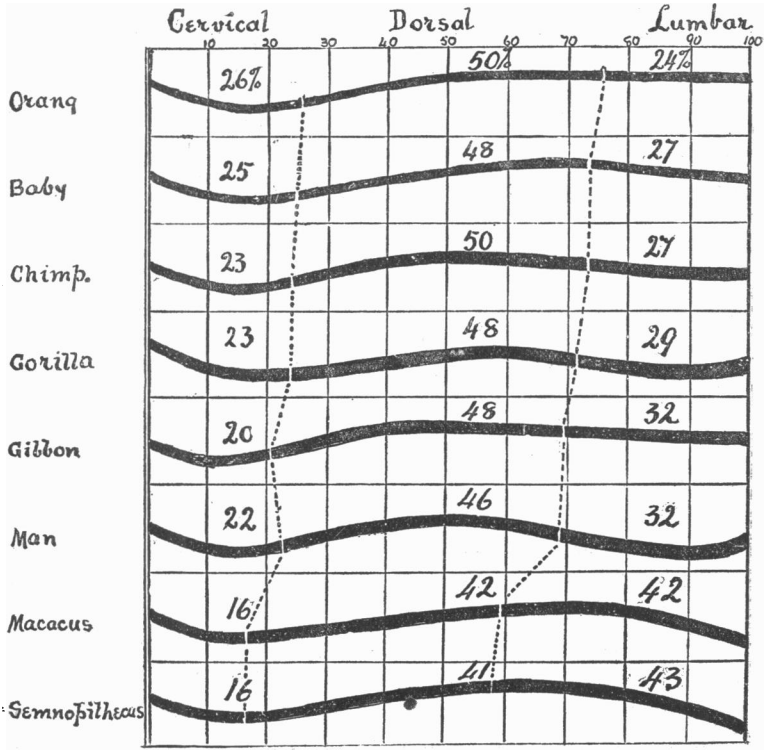

FIG. 4.—Diagram to show the relative proportions of the cervical, dorsal, and lumbar regions of the spinal column of the Higher Primates.

also applicable to the gorilla and chimpanzee—is owing to its brachiating habit of progression. While its arms and the upper half of its trunk are greatly developed, the lower half of the trunk and lower extremities are small and out of proportion.

The cervical and dorsal regions of the spine retain practically

the same relative proportions in all the orthograde primates. The apparent shortness of the neck in pronograde apes is due to the relatively long lumbar region.

Summary.

With the evolution of the orthograde from pronograde primates, the lumbar region becomes relatively shorter, the process of abbreviation being brought about by the transformation of the 26th (lumbar) segment to the 1st sacral; in the evolution of the giant primates (the ancestral stock of man, the gorilla, chimpanzee, orang), the lumbar region was further shortened, the 25th segment becoming gradually sacral in character. In the origin of the human stock, by the assumption of plantigrade progression, the lumbar region again became elongated, and it is possible that there may be in progress a slight backward migration—a tendency for the 25th to again become lumbar in character; but the fact that the point at which sacralisation commences is situated more distally in the negro than in the white man is against this assumption. In the evolution of the orang the lumbar region was further shortened, the 24th segment becoming sacral in character. That is the working theory which I put forward to account for the segmental arrangement of vertebræ and nerves in the Higher Primates.

All the data given here support Rosenberg's conception that in comparing two animals, the 19th segment of one corresponds to the 19th of the other, and the 20th to the 20th; that one segment may assume one or all the characters of its neighbour on either side; that suppression or intercalation of segments has played no part in the evolution of the higher mammals. It is certainly true that unilateral division of a segment occurs; it is possible that the division may be occasionally bilateral, but such a division is comparable to the abnormal process of dichotomy that produces in the embryo a double digit or a twin monster.

The extensive series of specimens in the Warren Museum in Harvard University, described recently by Professor Dwight,

shows how every intermediate form occurs between the sacralisation of the 24th and of the 26th segments, and that it is not a matter of lifting out or inserting a segment, but the gradual transformation of the characters of one segment into those of the one lying next it in the series.

I gladly avail myself of this opportunity of acknowledging my indebtedness to Dr Charles Hose of Sarawak, who, at much personal sacrifice, has sent me an ample supply of primate material.

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