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MODIFICATIONS OF PATTERN IN THE AORTIC ARCH SYSTEM OF BIRDS AND THEIR PHYLOGENETIC SIGNIFICANCE

By **Fred H. Glenny**[1]

Introduction

My interest in the aortic arch system in birds was stimulated by the discovery of a functional left radix aortae in the belted kingfisher during a routine dissection of that bird in 1938. Subsequent studies on several other species of birds produced interesting anatomical information, and, with continued studies, a semblance of order in occurrence of carotid patterns became more and more evident.

After a reasonably large series of families and orders of birds had been examined, it appeared that further studies might produce information which could be of value in avian taxonomy. As a result, a series of systematic studies of the main arteries of the neck and thorax of birds was initiated and carried out over a period of about 12 years.

During the past 2 or 3 years important implications with respect to the evolution of the aortic arch system in the birds became more apparent, and the present treatise deals primarily with this aspect of my accumulated studies.

The classification of birds used in this study follows the arrangement of Wetmore and Peters, with only a minor revision in the listing of the parrots in the subfamily Psittacinae. In my opinion, the Wetmore and Peters classification of the birds of the world is more in accord with the natural relationships than are the schema employed by many of the European taxonomists.

Insofar as possible the names of birds as used by earlier and even contemporary writers have been checked as to synonymy with Peters' (1931–51) checklist. Since Peters' checklist is not complete

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for the Passeriformes, only the authority for the species listed can be given.

The British Museum catalog of birds and Sharpe's hand-list have been freely consulted in an effort to obtain information essential to the establishment of the names of species and subspecies synonymous with those in the Peters checklist.

Unless otherwise noted, only single specimens were studied; in instances where more were studied the number is noted after the species name.

I wish to express sincere gratitude to the following individuals and institutions for their generous assistance in making available materials used in the study, and for their many helpful suggestions and criticisms in the preparation of this paper: American Museum of Natural History; Chicago Natural History Museum; Cleveland Museum of Natural History; Fan Memorial Institute of Biology; Meems Brothers and Ward, Inc.; Royal Ontario Museum of Zoology; Sudan Government Museum, Natural History; United States National Museum; and Ward's Natural Science Establishment, Inc.; Dr. John W. Aldrich, Dr. Dean Amadon, Dr. Doris Cochran, Mr. J. W. Cowland, Dr. E. Horne Craigie, Dr. David E. Davis, Mr. Dwight D. Davis, Dr. Charles A. Dambach, Mr. R. N. Deaton, Dr. E. H. Dustman, Dr. Herbert Friedmann, Dr. Ira N. Gabrielson, Dr. D. L. Gamble, Mrs. M. E. Glenny, Mr. W. Earl Godfrey, Dr. Walter C. Kraatz, Mr. W. J. Leach, Mr. Ben H. Morgan, Mrs. C. P. Mountz, Dr. Harry C. Oberholser, Dr. John W. Price, Dr. Loren S. Putnam, Dr. D. P. Quiring, Mr. Tsen-Hwang Shaw, and Dr. Alexander Wetmore.

Review of the literature

From shortly after the turn of the 19th century until its end, European anatomists and ornithologists evinced a considerable interest in the arterial system of birds. Among the earliest writers on this subject were Bauer, Meckel, Nitzsch, and Hahn, followed by Owen and Barkow. With the rapid expansion of interest in comparative morphology during the middle of the 19th century, other workers soon became engaged in numerous and very revealing investigations to which they tried to give some semblance of order and meaning. Prominent among this group of workers were Boas, Rathke, Sabatier, and Garrod.

During the middle of the 19th century, the theory of ontogenetic recapitulation was developed and became of considerable importance in the fields of comparative and human anatomy and organic evolution. It was during this time that the study of anatomy received its greatest impetus and achieved the peak of respectability in science.

Garrod, of all the workers of his time, was least successful in interpreting his findings, with the result that the significance of his contributions on the carotid arteries in birds was overlooked by most workers. Even Forbes and Beddard failed to interpret Garrod's studies satisfactorily, but Boas, Rathke, and Sabatier were better received by most of their contemporaries, with the result that many of their contributions and writings have been passed on to the present time. With respect to their interpretations of the arrangement in birds of the arteries and, especially, the aortic arches, they were incorrect in certain important details. Although Brenner had questioned Rathke's and Sabatier's placement of the subclavian artery as early as 1883, most textbooks in comparative anatomy still carry plates of the Rathke-Boas type of schematic diagrams.

In spite of correct information presented by Gadow, Hertwig, Hochstetter, and others, only a few textbook writers have made an effort to present the facts in preference to the presentation of a plan of organization or a pattern of evolution in the aortic arch system of the vertebrates.

A great deal of research was necessary even after the end of the 19th century in order to clarify the true nature of the aortic arch system and the changes which these and associated vessels undergo during embryonic development. The greatest single contribution of this kind was made at Northwestern University under the direction of W. A. Locy. Significant contributions on the embryonic development of arteries in birds were made during the first 6 years of the 20th century by Rabl, Sabin, Locy, and Twining. Thereafter, little work of importance reached the literature until 1934 when Hughes published his very important studies on the development of the cephalic blood vessels in the chick.

Despite these studies, a great gap still exists insofar as the development of the coracoid or sternoclavicular, thoracic or intercostal (internal mammary), and pectoral arteries of birds are concerned. I have been unable to find a single reliable account of the exact development of these vessels. Most anatomical references allude to the mammalian condition insofar as it is known, but actual accounts for birds appear to be lacking.

Apparently, there was little interest in the arterial system of adult birds (for well over a quarter of a century) until I began systematic studies of the arteries of the neck and thorax. Shortly thereafter Bhaduri and Biswas began a similar series of studies in India, and a few other incidental papers have appeared from time to time, treating largely with anomalous occurrence of vestiges of embryonic vessels.

As a result of these studies, I feel that it is well to summarize the findings of earlier and present-day workers in such a way that future workers may be better able to interpret their findings. It is with this in mind that I propose to discuss the significant changes in the aortic arch system and associated vessels with respect to their ultimate fate in birds.

It must be recognized that much of the present interpretation cannot be entirely resolved without further and extensive embryological studies on the nature of the origin and development of these vessels in the various orders, families, and species of birds. The complexities arising from important differences in the final arrangement-patterns of the arteries in the neck and thorax add considerably to the difficulties of interpretation. As a result, much of the interpretation will of necessity be quite generalized. Furthermore, this interpretation is based largely upon the studies made on the chick embryo, and since there probably are a great many important differences to be encountered in other orders of birds, the present interpretations may not be entirely accurate in at least some of the details.

It is suggested that renewed efforts be made to carry out embryological studies on the development of birds other than the chick, and that the development of the aortic arch system be given especial attention. Among the more critical aspects of this study are the manner and time of fusion of the anterior dorsal radices aortae (dorsal carotids), the manner in which the proximal portion of the dorsal radix, anterior to the carotid arch, atrophies, and the changes in and the fate of the ventral radices aortae (ventral carotids).

Another factor which should be taken into consideration is that of interpretation of the diagrammatic representations of structure, especially since there are apparent changes in the spatial relationships of portions of the aortic arch system in the different vertebrate groups, and these changes may be brought about as a result of other structural changes or modifications. Some of these structural modifications appear to produce an anterior-posterior compression or contraction of the aortic arch system with corresponding changes in the definitive spatial relationships of the early embryonic system. In the amniotes, and especially in birds and mammals, the ventral aorta appears to be lost, and the ventral radices aortae or ventral carotids are greatly modified. Such a modification in the structural-spatial relationship is rather advanced in the human embryo, with the result that interpretation of true homologies is sometimes very difficult.

Too frequently schematic or diagrammatic representations are or may be misleading as a result of faulty interpretation of both the diagrams and the actual condition as critically observed in study materials. Interpretation of the materials under study, however, should be facilitated by a careful study and analysis of the schematic diagrams. When this has been done, barring the lack of important embryological facts, there should be little difficulty in making adequate and correct interpretations.

As an aid in the interpretation of the adult avian aortic arch derivatives, it is well to make comparisons with the aortic arch derivatives in the other tetrapod vertebrates, and to attempt to show homologies such as do exist.

Early development of the avian vascular system

In discussing the early development of the vascular system of the chick, Patten (1929) states that the early vessels are formed from mesodermal cells that lie in the path of their development and that the walls of these early vessels are one cell-layer in thickness. As a result, no clear structural differences between the precursors of both arteries and veins arise until a much later period in development. Balfour (1873) has stated that the blood vessels of the chick arise not as spaces or channels between the mesoblast cells but as a network formed by united processes of the mesoblast cells, and that it is through these processes that the blood flows. He also stated that first traces of blood vessels are to be found in the pellucid area at about 30 hours of incubation.

Hyman (1942) states that the blood and blood vessels arise from mesenchyme cells of the mesoderm by forming patches of cells and that the central cells become modified into blood corpuscles, while the peripheral cells become oriented so as to form tubes, the early blood vessels. Essentially all these views represent the same concept, but expressed in slightly different ways.

The vitelline veins are the earliest vessels to form in the embryo and are found to develop on the surface of the yolk sac in the splanchnic hypomere and then pass to the embryo in the gut mesentery and finally come to enter the heart at its caudal end.

The ventral aorta is observed to arise at the cephalic end of the heart, with which it then becomes connected. The ventral aorta then extends anteriorly to the anterior end of the pharynx, at which point it bifurcates to form the anlagen of the ventral radices aortae, which then turn laterally and dorsally and pass around the pharynx, on either side, and curve posteriorly, dorsal to the pharynx, as the dorsal radices aortae which carry the blood backwards to the vitelline arteries which in turn pass to the yolk sac. Thus the first aortic arch which now lies within the mass of the mandibular visceral arch comes to be the first of the true aortic arches formed. Subsequently five additional pairs of vessels communicating between the ventral and dorsal radices aortae come into existence for a varying length of time, depending upon their ultimate fate in the adult bird and the function which they serve in the embryo or in the adult. Later, the two dorsal radices aortae, posterior to the pharyngeal region, come to fuse, thus forming the single median dorsal aorta (abdominal aorta) of the adult vertebrate.

Jolly (1940) has pointed out that the origin and mode of formation of the large embryonic vessels is still a matter in question and cloaked in obscurity, but he supports the view that the aortic vessels form *in situ* and are not the result of a "budding" or outgrowth from the heart nor a product of "migration," but rather are independent in origin and formation from the heart. Hyman (1942) asserts that a tubular cavity arises on either side (in the embryo) in the splanchnic

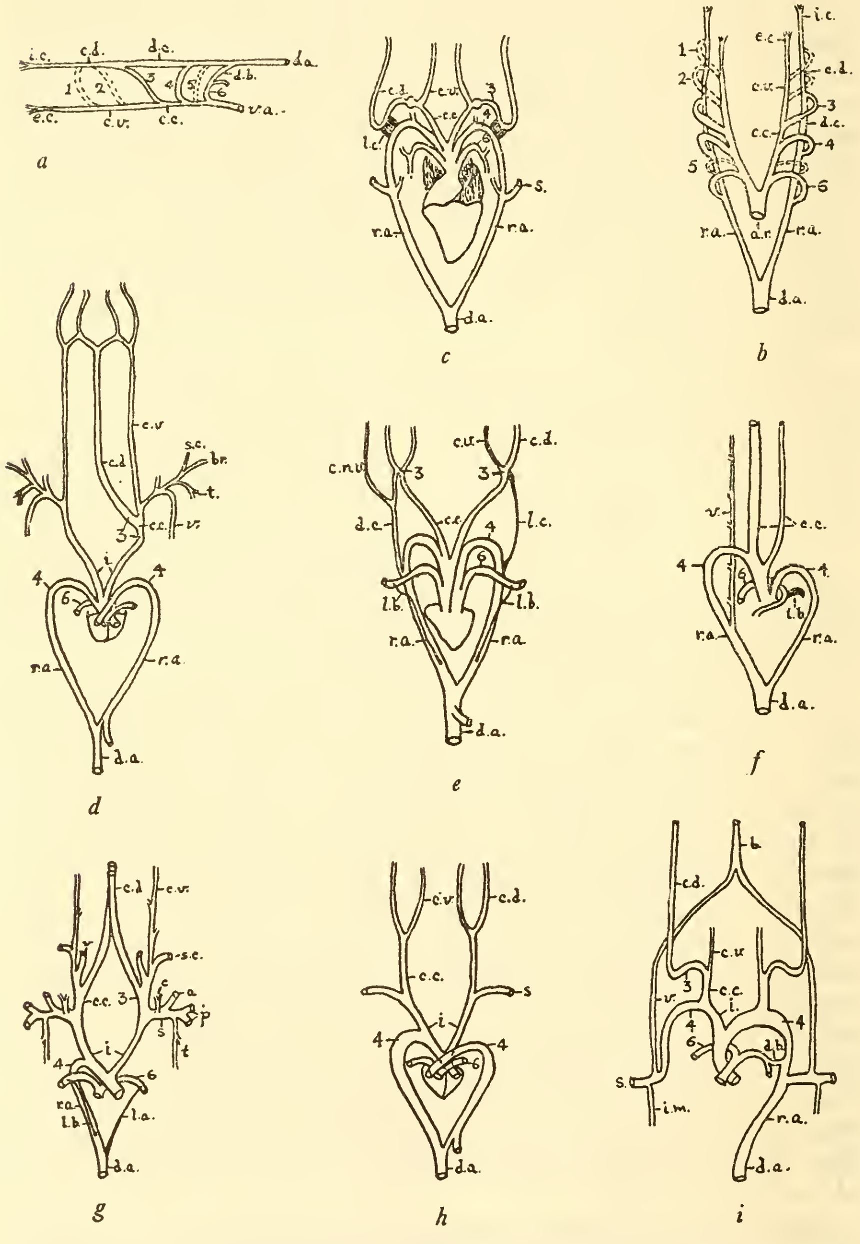

FIGURE 108.—For explanation see facing page.

mesoderm of the hypomere, and is of the same nature as the blood vessels, and that, as the hypomere closes below in the median ventral line, the two cavities are brought together and fuse to form the heart. With the disappearance of the ventral mesocardium the heart comes to lie free in the coelom.

Patten (1939) points out that the paired ventral aortic roots extend anteriorly from the bulbo-conus arteriosus (anterior heart chamber), and that the ventral aortic roots and the omphalomesenteric veins constitute direct continuations of the paired endocardial primordia of the heart. This is not in contradiction to Jolly's view of vessel formation within the embyro.

At about the 44-hour stage of incubation the heart begins regular contraction, thus establishing the circulation of the blood.

In birds and mammals the ventricle is divided into left and right compartments by the interventricular septum. The atrium is likewise divided by the interatrial septum, and the sinus venosus, still recognizable, is incorporated into the wall of the right auricle according to Quiring (1933). The systemic or aortic root and the pulmonary root form by a splitting of the conus arteriosus into two main trunks. The aortic or systemic root passes from the left ventricle to the body, while the pulmonary root passes from the right ventricle to the lungs. Thus the bird heart is comprised of two embryonic chambers, each of which is secondarily divided into two compartments, while the other two heart chambers of the lower vertebrates and the chick embryo are lost through incorporation and further structural and functional modifications. The atrium and ventricle of the early embryonic heart alone persists as the primary heart chambers, and the valves of the conus arteriosus persist in the pulmonary and systemic roots at the point of junction of these vessels with the ventricles.

As reported by Twining (1906), Lillie (1908, 1919), Patten (1929), Hughes (1934), and others, the aortic arches make their appearance (in the chick embryo) in order and at approximately the following levels of development or incubation: (1) first aortic arch appears in

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FIGURE 108.—*a*, Amniote aortic arch arrangement, lateral view; *b*, same, ventral view; *c-i*, ventral views of main cervical and thoracic arteries; *c*, in *Bufo melostictus* (modified after Bhaduri); *d*, in *Alligator mississippiensis* (modified after Reese); *e*, in *Sphenodon punctatus* (USNM 19260); *f*, in *Boa constrictor* (after Hafferl); *g*, in birds (generalized); *h*, in *Emys* (modified after Hafferl); *i*, in mammals (modified after Patten). Explanation of symbols: 1–6, aortic arches; a., axillary artery; a.r., aortic root; b., basilar artery; br., brachial artery; c., coracoid artery; c.c., common carotid artery; c.d., dorsal carotid artery; c.v., ventral carotid artery; c.n.v., comes nervi vagi; d.a., dorsal (abdominal) aorta; d.b., ductus botalli; d.c., ductus caroticus; e.c., external carotid artery; i., innominate artery; i.c., internal carotid artery; i.m., internal mammary artery; l.a., ligamentum aortae; l.b., ligamentum botalli; l.c., ligamentum caroticum; p., pectoral arteries; r.a., radix aortae; s., subclavian artery; s.c., subscapular artery; t., thoracic artery; v., vertebral artery; v.a., ventral aorta.

from 33 to 38 hours of incubation and disappears about the third or fourth day, or by the 32-somite stage; (2) second aortic arch appears at about the end of the second day and at least by the end of 50 to 55 hours of incubation, and disappears during the fourth day or by about the 32-somite stage; (3) third aortic (carotid) arch is usually present by the end of the second day or by the end of 50 hours of incubation, and this vessel usually remains throughout the life of the bird, although it may be modified in part in the adult where it forms, at least in part, the common carotid artery; (4) fourth aortic (systemic) arch arises in the embryo during the third day of incubation and is present by the end of 72 hours of incubation; the right arch alone (normally) remains and serves as the functional systemic arch connecting the systemic root with the dorsal radix aortae on the right side; the left arch is reduced by about 6½ days of incubation, and usually entirely obliterated by 7½ days of incubation; (5) fifth aortic arch is a transient vessel which makes its appearance during the first half of the fourth day of incubation and disappears by about the end of the fifth day; (6) sixth aortic (pulmonary) arch makes its appearance usually by the end of the fourth day and persists, at least in part, for the duration of the animal's life; the proximal ends of both vessels remain but become connected with the new pulmonary artery, which forms *de novo in situ* and supplies the lung; the distal portion atrophies and the left ductus arteriosus (botalli) usually completely disappears, while the right remains in many birds as the ligamentum botalli or it may fuse with the ventral face of the right radix aortae where it appears as a white streak (linea botalli) along the ventral face of the radix; (7) internal carotid artery appears at about the beginning of the third day of incubation as an anterior prolongation of the dorsal radix aortae from which point it extends into the head region, in rather close association with the brain.

Early changes in aortic arches

As has already been noted, the first, second, and fifth aortic arches become obliterated at an early stage in the embryonic life of the bird. According to Lillie (1908), these deletions occur on the third and fourth days of incubation in the case of the first two aortic arches, and, as has been pointed out by Hughes (1934), the fifth arch tends to disappear during the fifth day of incubation.

During the sixth to seventh day of incubation the fourth aortic arch of the left side loses its connection with the truncus. At this same time the dorsal connection between the fourth and third left arch (ductus caroticus) becomes reduced and soon loses its attachment with the left fourth aortic arch. By the 7½-day stage there is no trace of the left systemic arch except in instances of anomalous retention such as those cited by Biswas (1946) and Pohlman (1920). The dorsal radix aortae of the left side then anastomoses, medial to the ductus botalli, to the proximal portion of the pulmonary arch. As has been demonstrated (Glenny, 1943b, 1943d, 1944d), this secondary attachment precedes atrophy of the ductus botalli of the left side, and the left radix aortae posterior to the left fourth aortic arch begins to take over the function of the ductus botalli of that side.

No accurate account of the loss of the ductus caroticus of the right side could be located. It may be assumed that this occurs first as a disconnection at the level of the right systemic arch and perhaps may occur much later than has been suspected. Bhaduri (1939), Finn (1891), Glenny (1944a), Mathew (1944), and Subhapradha (1944) have reported the persistence of the ductus caroticus on the right side of several birds. Rarely, however, the otherwise functionally modified ductus caroticus may retain a short ligamentous connection with the right systemic arch (Glenny, 1944a). It has been inferred that the ductus shawi represents a functionally modified ductus caroticus which comes to serve as the supply to the bronchi, and sends off branches to the syrinx, lung substance, and the oesophagus (Hafferl, 1933). Not altogether satisfactory studies have been made on the exact changes which take place in the ductus caroticus.

The fact that the right dorsal radix aortae remains as the functional vessel carrying blood to the abdominal aorta does influence the subsequent history of the right ductus botalli. This vessel remains functional almost throughout the embryonic life of most birds, and undergoes further atrophy subsequent to hatching. While most orders of birds retain at least a ligamentous vestige of this embryonic vessel, many families show a greater degree of atrophy of this structure than do others. In some species where obliteration is nearly complete there is frequently evidence of its persistence as a linea botalli along the ventral face of the dorsal radix, with which structure it may fuse.

With the atrophy of the right ductus botalli, the left radix aortae begins to atrophy. This process continues in most birds until only a small ligamentum aortae remains as the vestige of this once prominent vessel. Rarely, the left radix aortae may remain as a functionally modified vessel (Glenny, 1939) or, more frequently, with a short lumen. In general it may be stated that almost without exception extremely careful examination of the adult bird will reveal a minute ligamentous vestige of the left radix aortae. The difficulty encountered in determining its presence arises from the fact that the ligament may become so much reduced that it is difficult to differentiate it from the surrounding fascia, and in smaller birds it is still more difficult to find.

When the right ligamentum botalli is much reduced, its distal attachment to the radix aortae may be determined by the presence of a small ligamentous button on the ventral face of the right radix.

The systemic arches in birds are paired structures only during early embryonic stages. Biswas (1946), however, reported the anomalous occurrence of both left and right systemic arches in a specimen of *Ploceus philippinus philippinus*.

Normally, atrophy of the left systemic arch follows shortly after the disconnection of the ductus caroticus from the posterior portion of the dorsal radices aortae. This results in the retention of the right systemic arch as a functional vessel which then passes diagonally lateral and dorsad to join the remaining functional right dorsal radix aortae which then passes diagonally toward the midline to the point of union with its complementary vessel of the left side. The latter vessel is usually found in the adult as the ligamentum aortae. The functional radix then forms a connection with the abdominal aorta.

In the respect that birds present but one of the pair of systemic arches, they differ from mammals. On the other hand, the right dorsal radix aortae in birds and the left dorsal radix aortae in mammals are the sole functional vessels which are responsible for the distribution of the blood to the abdominal viscera and posterior appendages.

As is well known, the ventral or proximal portion of the embryonic sixth aortic arch remains as the functional portion of this embryonic vessel which, along with the embryonic pulmonary artery that joins it, comes to serve as the definitive pulmonary artery of the adult.

The left ductus botalli usually undergoes atrophy shortly after the complete atrophy of the left systemic arch, by which time the left radix forms an anastomosis with the pulmonary arch proximal to the normal dorsal (ductus botalli–radix aortae) connection. As a result of this secondary connection, the left dorsal radix aortae serves the same function as the ductus botalli (Glenny, 1943d, 1944d). This is not the case in anomalous retention of the left systemic arch as reported by Biswas (1946). In this rather singular case, the distal portion of the left radix atrophied and the connection was maintained by way of the left systemic arch, and the left ligamentum botalli remained as the vestige of the embryonic vessel, whereas in most cases the left ligamentum botalli completely atrophies, or at best becomes fused with the left radix aortae either prior to or at the same time as the radix undergoes atrophy.

In instances of functional modification of the left radix aortae, the left ligamentum botalli may or may not be completely lost; but this is extremely difficult to ascertain since so few species or individuals may retain a functional left radix aortae and atrophy of the ligamentum botalli has usually progressed to such a stage that determination of its presence is difficult.

The distal portion of the right sixth aortic arch undergoes atrophy and becomes the ligamentum botalli or it may rarely maintain a small lumen. In such instances where it does not appear to be present it may fuse with the radix and be completely lost or remain as a linea botalli, or it may be partially resorbed and remain as an incomplete ligament or as a ligamentous button on the ventral surface of the radix aortae.

Atrophy of the right ductus botalli and the left radix aortae occurs at approximately the same time and at about the same rate. It appears that, as in many species of birds, there may be a continued progressive atrophy of both of these structures for quite a time after hatching. The rate and level of atrophy of these structures may differ in different species, but particularly between families and orders of birds. It appears that, in a few orders and families of birds, atrophy of these two structures may be independent of each other. This assumption is based on observations on many species within a family or order in which the ligamentum aortae may be of considerable size, while the right ligamentum botalli is almost entirely or completely lacking or remains as a linea botalli.

Much confusion and misunderstanding is encountered in the literature with respect to the carotid arteries. This is in part due to the lack of uniformity in terminology and to the failure to recognize some definitive vessels which are embryonic derivatives. Incomplete series for study, along with inadequate techniques, account in part for the failure of earlier workers to fully comprehend the significant changes which occur during the first week or 10 days of incubation. Furthermore, many of the earlier workers probably were greatly influenced in their views and interpretations by the dominant concept of ontogenetic recapitulation which so strongly influenced the studies of morphologists during the 19th century.

Some authors refer to the dorsal and ventral radices aortae simply as the dorsal and ventral carotids. This may have led to some misinterpretation, since the internal and external carotids are sometimes referred to as the dorsal and ventral carotids. Interpretation is difficult because direct comparisons cannot be made between birds and reptiles on the one hand or between birds and mammals on the other hand since the development of these vessels differs somewhat in details in each of the three classes of amniotes.

According to Twining (1906), the third aortic arch gives rise to a dorsal carotid and a ventral carotid; the former is well developed and easily traced anteriorly, while the latter, which he regards as the basal remnant of the first and second aortic arches, arises from the base of the third arch. At this early stage no trace is found of a vessel connecting the dorsal and ventral carotids, the entire blood supply to the jaw anlagen being produced by the ventral carotids. Anastomosis of the dorsal and ventral carotids occurs during a later stage in the embryonic development.

Increase in length of the dorsal and ventral carotids results from elongation of the cervical region, and this is followed by many complex changes in the arrangement and orientation of the other associated vessels.

In the 5½-day chick a vessel arises *de novo* from the dorsal carotid at a point about halfway between the third arch and posterior border of the eye. At a later stage this vessel comes to communicate with the ventral carotid, thus forming the fork of the external carotid.

Mackay (1887) maintains that the ventral carotid does not contribute to the formation of the external carotid, but Twining (1906) and Hughes (1934) have shown that Mackay's conclusions were incorrect.

With elongation of the carotid arch, the ventral carotid comes to assume a somewhat more dorsal position, and in the 6½-day chick embryo the secondary subclavian artery forms an anastomosis with the third arch somewhat ventral to the ventral carotid. Consequently, Mackay's contention that the definitive subclavian and the ventral carotid join in a common stalk is not substantiated by Twining's study.

The dorsal carotid and anterior branches of the ventral carotid undergo an anastomosis between the sixth and seventh days of incubation. This connection results in a dual blood supply to the upper and lower jaws. The portion of the dorsal carotid anterior to the anastomosing branch is referred to by Twining as the internal carotid.

In the chick embryo of 7 to 8 days, the ventral carotid is reported to lose its anterior connection. The carotid arch elongates anteriorly, and with this there is a dorsal and anterior migration of the thyroid gland.

Twining states that the vertebral is generally a branch of the common carotid. Glenny, in a long series of systematic studies, has shown that the vertebrals may vary considerably in the point of origin (dorsal radix anterior to the third arch, the common carotid, or as a branch of the superficial cervical or ventral carotid).

With the interruption of the ventral carotid at a point about midway between the basal portion of the third arch and the cephalic end of the external carotid (Hughes, 1934; Twining, 1906) the entire blood supply to the head (other than that carried by the vertebrals) traverses the dorsal carotids. The earlier communicating vessel, which connects the dorsal and ventral carotids, then comes to supply the vessels which were previously connected with the ventral carotid. Both Twining and Hughes have demonstrated that the anterior or cephalic portion of the ventral carotids function as descending oesophageal arteries. This corresponds with Glenny's (1944d) findings on the Canada goose. Thus the shunt which develops between the dorsal and ventral carotids during the sixth and seventh days of incubation in the chick embryo serves to carry the cephalic blood supply previously carried by the ventral carotid.

While Twining considered the proximal portion of the ventral carotid to degenerate or atrophy, Hughes, in his studies on the 9-day chick and subsequent stages, points out that this portion of the ventral carotid becomes functionally modified to form the ascending oesophageal artery. This view is likewise shared by Glenny (1944d). It should be pointed out that in several orders of birds this functionally modified vessel may be short and greatly reduced, with the result that during its development it may be readily overlooked and even in the adult bird may be detected only after the most careful examination or upon injection with colored materials. Bhaduri and Biswas (1945, 1947, 1954) have shown that it may be continuous, and retain its natural connection. I have observed the superficial cervical artery to be continuous and uninterrupted for the entire length of the neck in several orders of birds. This is probably the basic or ancestral arrangement, whereas the discontinuity of these ventral carotids is probably a modification rather than the usual condition.

At about the eighth to ninth day of incubation the innominate artery may be recognized as originating from the basal portion of the third aortic arch.

Therefore, it may be seen that (1) the innominate arteries are derived from the basal portion of the third arch; (2) the vessel from the point of junction with the subclavian to the region of the thyroid gland represents, for the most part, the dorsal portion of the third arch; and (3) the vessel lying beyond this point up to the base of the head represents the dorsal radix aortae, anterior to the third arch.

The origin and development of the cephalic branches of both the internal and external carotid arteries are extremely well treated by Bauer (1825), Hughes (1934), Ottley (1879), Twining (1906), and others in both general and specific studies on the vascular system of birds. Hughes has pointed out that there are several important differences in the connection of the cephalic branches of the external and internal carotids between birds and mammals and, as a result, there cannot be a direct transfer of information from one group to the other. An exposition of these differences is of no great significance in this study.

The ventral radices aortae (ventral carotids), as has been noted, may become functionally modified to form the ascending oesophageal artery from the posterior portion of the ventral carotids and the descending oesophageal artery from the anterior portion of this same vessel after disjunction. The external carotid, as a result, receives blood by way of the dorsal carotid artery subsequent to the disjunction. It is possible that extensive reduction of the proximal portion of the ventral carotid may result in a very short and much reduced ascending oesophageal artery in many families of birds, while in still others it is a prominent structure.

Hafferl (1933) points out that the subclavian artery in birds is not the primary blood vessel which is formed at first in the embryo but that it arises from the ventral part of the third aortic arch, so that in the adult animal a common trunk with the carotid artery exists as the innominate artery.

The axillary artery is derived from the distal portion of the primary subclavian artery.

Hochstetter (1890) has shown that the definitive subclavian arises from the ventral ends of the carotid arches, as had previously been announced by Mackay (1887), but that the primary arteries to the wing-bud have their source directly from the dorsal aorta, as segmental vessels, and that the primary subclavian then completely disappears. This primary vessel was regarded by Hochstetter as the mammalian homologue. Sabatier (1874), Rathke (1850), and others tended to add confusion to the matter by misplacing or improperly locating the definitive subclavian, and it was not until Mackay and Hochstetter published the results of their studies that any true light was thrown upon the problem. In 1883, Brenner challenged the views of Rathke and Sabatier by pointing out that owing to the difference in the relative position of the vagus nerve, superior vena cava, and subclavian, the latter in birds could not correspond in a dorsal mode of origin with the subclavian of mammals.

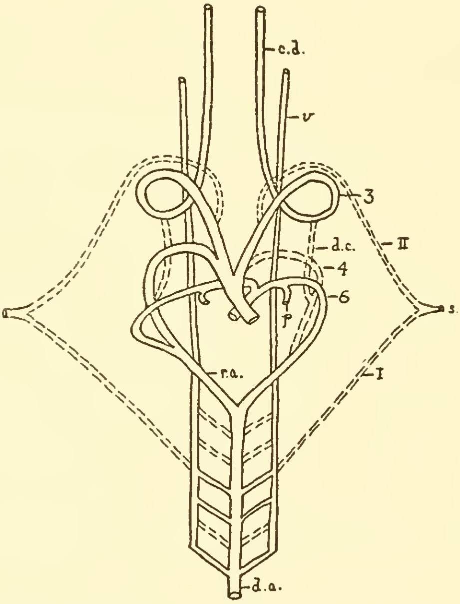

Figure 109.—Aortic arch system in *Gallus*, showing primary and secondary subclavians (ventral view, modified after Krassnig). Explanation of symbols: I, primary subclavian artery; II, secondary subclavian artery; 3, carotid arch; 4, systemic arch; 6, pulmonary arch; c.d., dorsal carotid artery; d.a., abdominal aorta; d.c., ductus caroticus; r.a., radix aortae; s, subclavian artery; v, vertebral artery.

Hochstetter's work demonstrated that, although the definitive vessel arises as a branch from the ventral part of the carotid arch, there is also present a branch from the dorsal aorta to the anlage of the wing, and that this latter vessel precedes the appearance of the secondary or definitive subclavian artery. The secondary subclavian makes its appearance on or about the sixth day of incubation, while the primary subclavian appears on about the fifth day according to Hochstetter.

Evans (1909b) has shown that the segmental subclavians commonly occur in the 16th to 19th intersomitic spaces. Hughes (1934) later pointed out that the segmental subclavian of the first intersegmental space enlarges at the expense of the others, and soon becomes the single dorsal subclavian artery although considerable variability in the primary subclavian development exists. Fleming's (1928) studies are largely confirmatory of Hughes' observations.

The two independently derived vessels (primary and secondary subclavians) come to form a junction on about the sixth day of incubation with the result that the limb-bud receives its blood supply from two separately derived vessels until about the eighth day, at which time the primary subclavian atrophies and finally disappears. Confirmatory studies on the origin and development of the subclavians in the chick were carried out by C. G. Sabin (1905). He reports that the primary subclavian begins to make its appearance at about 72 hours of incubation, and that by the first half of the fourth day the primary circulation is well established. He points out that the wing vessel is given off in common with the segmental artery on each side from a short dorsal branch of the aorta. Development of the secondary subclavian appears to take place from the primary subclavian forward and from the carotid arch backward. During the early part of the sixth day, Sabin reports the beginning of the formation of the ultimate subclavian from the carotid arch, where it arises from the anterior surface.

At the time of junction of the two subclavians the forelimb occupies a position posterior to the heart, with the result that the secondary subclavian has a comparatively long course to the limb. The major blood supply to the wing is still provided by the primary vessel until about the seventh day of incubation, at which time the heart begins to retrogress into the thorax, thus shortening the course of the secondary subclavian. During the latter part of the seventh day and early part of the eighth day of incubation the primary subclavian atrophies, although a distal vestige may remain for a short time as a small spur extending dorsally into the base of the wing from the secondary subclavian.

As the heart migrates posteriorly it gradually comes to lie in a position posterior to the wing. Consequently, the definitive subclavian becomes shortened and laterally directed. By the ninth day the condition in the embryo is similar to that in the adult.

As Hughes has emphasized, the metamerism of the nervous, muscular, and vascular systems serves as an aid in following changes which subsequently occur during the course of embryonic development. The first and second aortic arches are metamerically associated with the second and third pro-otic segments while the third aortic arch is associated with the first post-otic segment of the early embryo. Since the basal portion of the carotid arch in the adult is located at a position many segments behind the auditory capsule, it is considered that the aortic arches migrate posteriorly during the period of early development.

Prior to this migration, the embryo is a metamerically arranged structure with the segmental organs of the cephalic end in an undisturbed relationship (central nervous system with its nerve roots, somites, and aortic arches). At this time segmentally arranged intersomitic arteries and veins are to be found; however, with a change in this early segmental relationship and the caudad migration of the aortic arches, the roots of the intersomitic blood vessels become severed from the aorta and these vessels then anastomose longitudinally with one another to form the longitudinal vertebral artery. The newly formed vertebral artery later acquires new connections with the dorsal aorta; thus, its formation is dependent upon the posterior migration of the heart and the ultimate position of the aortic arches.

Formation of the subclavians and vertebrals are, as a result of the caudad migration of the heart and aortic arches, intimately related and it is likewise possible that the formation of the secondary external carotid may be closely dependent upon this same modification.

As noted by Hughes, the third aortic arch has migrated backward through 20 segments by the first half of the seventh day of incubation. The carotid arch in its final position lies opposite the 15th cervical ganglion, and the root of the common cervical artery (Fleming, 1926) lies opposite the 18th interspace, where it joins with the persistent intersomitic artery of this interspace. As a result, the distal portion of the vertebral root is derived from the same position as the primary subclavian artery.

Anteriorly the vertebral artery becomes connected with the external carotid by way of a deep branch of the occipital artery which runs between the occipital arch and the atlas.

In the pig, the internal mammary artery is formed by longitudinal anastomosing of the more cephalic of the thoracic intersegmental arteries caudad to the subclavian artery, and subsequent deletions of the proximal parts of the other intersegmentals leave it to arise from the subclavian. The origin is quite similar to that of the vertebral artery anterior to the subclavian. In the bird, however, the so-called internal mammary (thoracic or intercostal) artery does not appear to form in the same manner as in the mammal. Insofar as I can determine, no specific study has been made of the origin and development of this vessel and the other pectoral arteries.

Anterior intercostal supply is derived from the ventrally located vessels, variously named, that arise as branches of the subclavian arteries. There are no segmentally arranged vessels arising from the right posterior radix aorta as in mammals. Posteriorly, the intercostal muscles are supplied by segmentally arranged arteries which arise as branches of the abdominal aorta. No connection with posteriorly located arteries could be established, and it is presumed that the so-called internal mammary is not homologous with that of mammals but is an intercostal artery not homologous with the intercostals of mammals.

The above observations were made possible by materials especially prepared for this study by Ward's Natural Science Establishment. Three-day chicks were doubly injected with colored plastic and the entire birds were then treated with corrosive solutions. As a result of this treatment, it was found that the left radix aortae could be injected for about half of its normal length.

Changes in arrangement of thoracic and cervical arteries

In birds, several significant changes may take place during the course of embryonic development of the individual aside from and in addition to (1) loss of the first, second, and fifth aortic arches, (2) loss or functional modification of the ductus caroticus, (3) loss of the left fourth aortic arch, (4) atrophy or functional modification of the left radix aortae, (5) atrophy or loss of the ductus botalli, (6) the shunt anastomosis between the dorsal and ventral carotids (anterior radices aortae), and (7) the accompanying functional modification of the posterior end of the ventral carotid into an ascending oesophageal or superficial cervical artery and the anterior end of this same vessel into a descending oesophageal or superficial cervical artery.

The dorsal carotids usually migrate to a median ventral position along the long axis of the cervical vertebrae and, with the development of the ventral cervical musculature, soon become enclosed within the hypapophysial canal. These vessels then follow the course of this canal to a point near the site of articulation between the third and fourth cervical vertebrae, where they emerge and send off branches comparable to those which join the internal and external carotid arteries.

It should be noted that in most orders and families of birds the right dorsal carotid artery comes to lie in a position dorsad to the left dorsal carotid artery, within the hypapophysial canal. This particular orientation of the carotids may be attained as a result of the growth of the ventral cervical muscles and their encroachment upon the space occupied by the carotids within the hypapophysial canal. Further reduction in size of the hypapophysial canal, by the encroachment of the aforementioned cervical muscles, may account, in part, for the fusion of the two carotid arteries and the resulting formation of the unicarotid arrangement.

While I have noted this orientation of left and right carotids within the hypapophysial canal many times, Bhaduri and Biswas (1954) have made particular mention of the condition.

Commonest of the modifications which occur because of the position of the dorsal radices (dorsal carotids) is that of fusion of these vessels between the third arch and the base of the head. As a result of this fusion of the two primary dorsal carotids, a single vessel traverses the length of the neck. In some orders of birds the basal portion of both vessels are present, while in other orders or families only the basal portion of one of the conjugate vessels is present. In still other instances, a vestige of the atrophied vessel remains as evidence of its earlier embryonic relationship in the system. When both basal portions of the conjugate vessel are present they may be equal or one side may be reduced in diameter. At the cephalic end of the conjugate carotid both left and right carotids are given off before they further divide into the several internal and external branches. These branches, as Hughes (1934) has pointed out, are not the same for birds as for mammals.

Reduction in the lumen of the basal portion of the dorsal carotids may occur on either side, and still further alteration in this portion of the carotid may occur in the form of atrophy, with retention of either a complete or an incomplete ligament. Insofar as I can determine, this ligament has never been described in any of the literature heretofore, and no name has as yet been assigned to it. Ottley (1879) described the presence of two white imperforate cords lying within the hypapophysial canal of *Bucorvus abyssinicus.* These he believed to be the remnants of the dorsal carotids. In recent studies I have had the opportunity of observing the same or similar structures which are definitely the ligamentous vestiges of the dorsal carotids. Since these structures were originally noted by Ottley, it would be well to refer to them as the ligamenti ottleyi. In forms which present ligaments on both sides (ligamenti ottleyi), the blood supply to the head is carried by enlarged vertebral and superficial cervical arteries.

When the paired dorsal radices aortae (anterior) do not enter the hypapophysial canal, the dorsal carotids may become further modified and may be reduced in size. In both *Zanclostomus javanicus javanicus* and *Phaenicophaeus pyrrhocephalus* the dorsal carotids were found to be superficial vessels, much reduced, and functionally modified as oesophageal arteries in addition to the normal function of cephalic blood supply. In *Rhamphococcyx curvirostris erythrognathus* the left dorsal carotid was superficial and modified to form an oesophageal blood supply while the right vessel was reduced to a ligamentum ottleyi. Both dorsal carotids have been found to be present as ligamenti ottleyi in *Bucorvus abyssinicus* and in *Rhopodytes viridirostris*.

Another variation in the arrangement of the dorsal carotids results from the superficial position of one of these vessels while the complimentary vessel lies within the hypapophysial canal. This is observed most commonly among the Psittaciformes, in which order the right carotid enters the hypapophysial canal while the left carotid is superficial and lies in close association with the vagus nerve of that side.

Some of the aberrancies noted among related species and genera emphasize the importance of geographical and ecological distribution of species, with the resultant specific and subspecific isolation as factors in the selection of successful types which may be found to present these anatomical variations. In addition to other factors, anatomical variations may, in conjunction with studies of geographical distribution, serve to show more clearly possible lineage within a family or order of birds on the one hand and possible routes of movement and dispersal in the course of evolution on the other hand.

The exact site of origin of the coracoid or sternoclavicular artery varies somewhat in different families of birds. Generally this vessel is found as a branch of the subclavian just medial to the axillary artery, but in a few orders it arises from different points on either the subclavian or the pectoral stem, and in some instances two, or rarely three, pairs of these vessels are present. In order to facilitate the classification of these vessels the following scheme is proposed:

Type A: coracoid artery is medial to the axillary.
Type B: coracoid artery is opposite the base of the axillary.
Type C: coracoid artery is lateral to the axillary.
Type D: two coracoids are present; one is medial or opposite the base of the axillary, the other is lateral to the axillary.
Type E: two coracoids are present; both are medial or opposite the base of the axillary.
Type F: two coracoids are present; both are lateral to the base of the axillary.

The thoracic, intercostal, or internal mammary artery of birds likewise is found to arise at slightly different relative positions—from a point at the base of the inferior pectoral artery to a point near the base of the coracoid or sternoclavicular artery, and in some instances both of these vessels have a common root from the subclavian artery. Such differences are found to be of common occurrence within several orders of birds. In the Galliformes and the Passeriformes there appears to be a graded series in the sites of attachment of the thoracic artery from a lateral to a medial position. As a result of these observations, numerical values can be assigned to the site of attachment of the intercostal or thoracic artery, and these values may come to be used as an index in specific levels of evolution. The following scheme is proposed for the classification of the thoracic arteries in birds:

Type 1: attachment to the pectoral stem lateral to the axillary.
Type 2: attachment to the subclavian between the axillary and coracoid.
Type 3: attachment to the subclavian at the base of the coracoid.
Type 4: attachment to the subclavian, but with a common root for both the coracoid and thoracic.
Type 5: attachment to the subclavian medial to both the axillary and coracoid.
Type 6: two separate thoracic arteries are present; the primary thoracic is the same as type 1 above, while the secondary thoracic is the same as type 3 or type 4 above.

The medial migration of the thoracic artery appears to have some phylogenetic significance as yet not understood.

Arrangements of dorsal carotid arteries

Insofar as the early embryonic stages in the development of the dorsal carotids are concerned, all birds may be considered to be bicarotid, but during subsequent stages in development many parts are deleted or functionally modified in an orderly sequence of events. As a result, higher-level deletions may be regarded as significant as indices of more recent derivation or of higher levels of species evolution, and with particular respect to the aortic arch system. Most recent evolutionary changes in the aortic arch system are related to the adult condition of the anterior dorsal radices aortae or dorsal carotid arteries.

Since the bicarotid condition is more primitive than the unicarotid condition, the former is to be considered as representing a lower level in the evolution of the system, and any variation of the unicarotid condition may be considered to represent an advance over the bicarotid condition. Within each of the main groups, however, there are certain special arrangements or modifications which may be regarded to be of additional value in determining relative positions within a family or order with respect to the evolution of the organ system.

A description of each of the known and anticipated arrangements of the dorsal carotid arteries is essential, and to clarify the classification of the carotid arrangement it is proposed that the bicarotid condition be referred to as Class A and the unicarotid condition be referred to as Class B. In addition, certain numerical values are assigned to the variations within each of these classes, and these numerical values may serve as indices of levels of evolution or specialization. Further, the letters *d* and *s* serve to indicate right or left side.

BICAROTID ARRANGEMENTS

1. Bicarotidinae normales: Both dorsal carotids enter the hypapophysial canal and pass anteriorly to the head without fusing. This arrangement is found in most orders of birds and is to be regarded as the basic arrangement.

2. Bicarotidinae abnormales: One of the dorsal carotids enters the hypapophysial canal, while the complimentary vessel of the opposite side remains as a superficial vessel. This condition is of infrequent ordinal occurrence but is very common among the parrots, in which group the right vessel enters the hypapophysial canal in most instances.
3. Bicarotidinae infranormales: Both dorsal carotids are superficial and lie along the ventral face of the neck. This condition is of rare occurrence. Despite the fact that it had been presumed to exist (Meckel, 1826), it was not discovered until 1952 when Glenny observed it in *Zanclostomus* and *Phaenicophaeus* and a further modification of it in *Ramphococcyx*. These vessels were found to send small branches to the oesophagus.

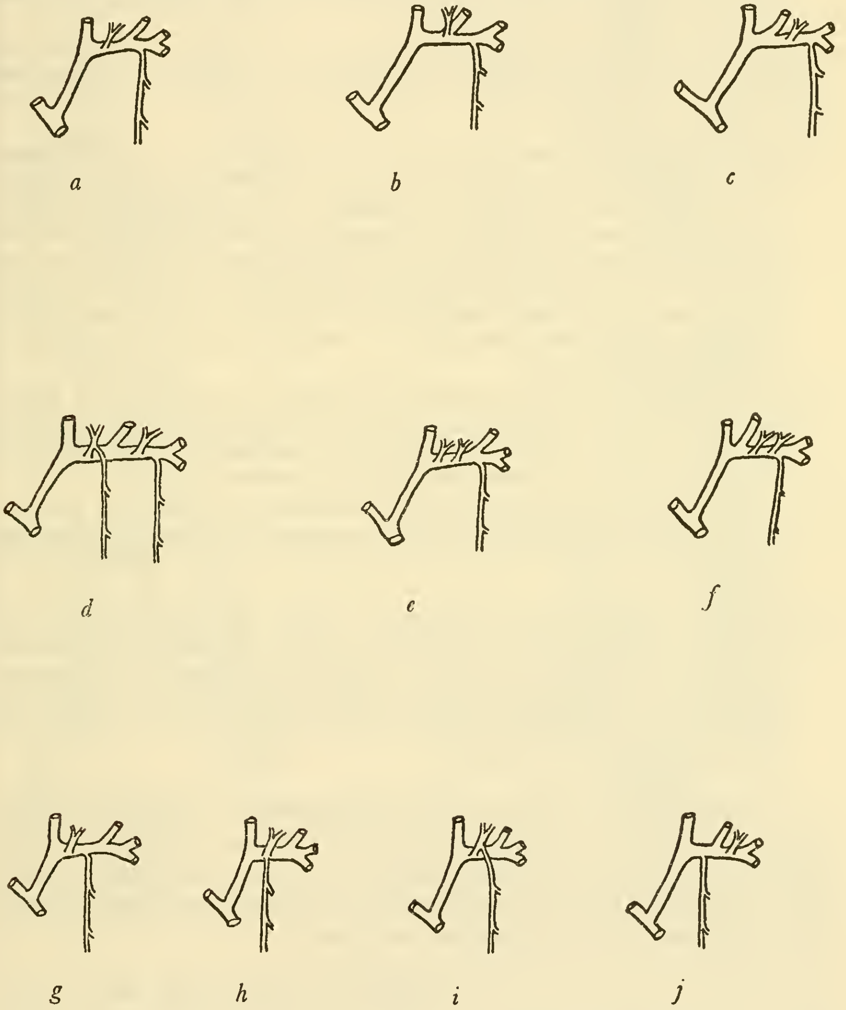

Figure 110.—Points of origin and types of the coracoid or sternoclavicular and thoracic or intercostal arteries (ventral views, left side only). Type of coracoid indicated by capital letter, type of thoracic indicated by numeral (for code see pp. 543, 544): *a*, A–1; *b*, B–1; *c*, C–1; *d*, D–6; *e*, E–1; *f*, F–1; *g*, A–2; *h*, A–3; *i*, A–4; *j*, C–5.

4. Ligamenti carotidinae normales (ligamenti ottleyi): Both anterior dorsal radices aortae (dorsal carotids) atrophy, but remain as the ligaments of Ottley and enter the hypapophysial canal. This is a condition of rare occurrence and has been observed in *Bucorvus* and *Rhopodytes.* This condition represents the culmination of the bicarotid evolution except for the unicarotid arrangements.

Unicarotid arrangements

1. Conjuncto-carotidinae normales: A single carotid artery enters the hypapophysial canal, but this is supplied by a pair of vessels of equal size from the common carotids of both left and right sides. This arrangement is quite common among the Ciconiiformes.
2. Conjuncto-carotidinae abnormales: The same as in 1, above, except that the basal vessel is reduced in diameter on one side. This is the first level in the modification of the conjugate carotid arrangement and is found in the flamingos and herons.
3. Ligamentum carotidinae-conjuncti: As in 2, above, or further modified except that the lumen of the reduced vessel is not complete and the distal portion of the basal vessel is reduced to a ligament. This condition is found to exist at two levels of atrophy: (1) second level modification results from atrophy at the anterior end of one of the basal vessels, but with a lumen for nearly half of its length, and (2) third level modification results from complete closure of the basal vessel with retention of a ligamentous vestige. This ligament may be entire or partial. The degree of resorption appears to vary in different species.
4. Laevo-carotidinae or dextro-carotidinae normales: The same as in 3, above, except that there is no remaining vestige of the ligamentous connection from the opposite side. This is the fourth level modification of the unicarotid arrangement and is commonly found in many orders of birds.
5. Laevo-carotidinae or dextro-carotidinae infranormales: The same as 4, above, except that the functional carotid is superficial and does not enter the hypapophysial canal. This has been reported in a single passerine genus, *Orthonyx.*
6. Ligamentum unicarotidinae (ligamentum ottleyi): The culmination of the unicarotid evolution results in atrophy of the single dorsal carotid artery. This may be at either of two levels: (1) retention of the ligamentous vestige, or (2) partial or complete resorption of the ligament. In such a case, the vertebrals and superficial cervical arteries will take over the function of supplying the blood to the head.

To simplify and codify the above classification of carotid arrangements, the following scheme is suggested; it may serve to indicate more nearly those close similarities and gross dissimilarities which may be presumed to exist and to indicate which orders of birds may be undergoing important anatomical evolution:

Class A

A–1	Bicarotidinae normales.
A–2–d	Bicarotidinae abnormales: right vessel superficial.
A–2–s	Bicarotidinae abnormales: left vessel superficial.
A–3	Bicarotidinae infranormales.
A–4	Ligamenti carotidinae normales (ligamenti ottleyi).

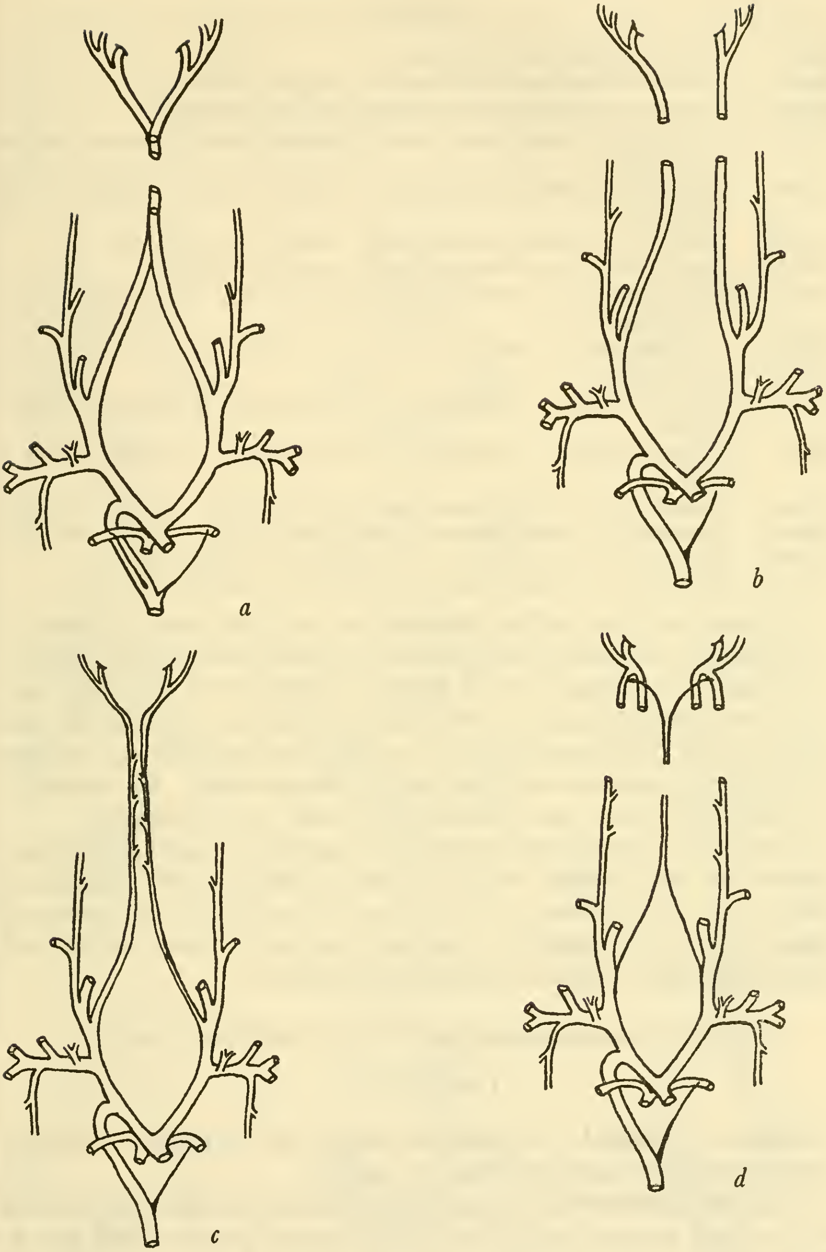

FIGURE 111.—Arrangements of the dorsal carotid arteries and the associated cervical and thoracic arteries in Aves Bicarotidinae (ventral views). Types (for code see pp. 544–546): *a*, A–1; *b*, A–2–s; *c*, A–3; *d*, A–4.

Class B

B–1	Conjuncto-carotidinae normales.
B–2–d	Conjuncto-carotidinae abnormales: right side reduced.
B–2–s	Conjuncto-carotidinae abnormales: left side reduced.
B–3a–d	Ligamentum carotidinae-conjuncti: partial lumen; ligament on the right side.
B–3a–s	Ligamentum carotidinae-conjuncti: partial lumen; ligament on the left side.
B–3b–d	Ligamentum carotidinae-conjuncti: entire, on right side.
B–3b–s	Ligamentum carotidinae-conjuncti: entire, on left side.
B–4–d	Dextro-carotidinae normales: right carotid alone enters the hypapophysial canal.
B–4–s	Laevo-carotidinae normales: left carotid alone enters the hypapophysial canal.
B–5–d	Dextro-carotidinae infranormales: right carotid is superficial (left is lacking).
B–5–s	Laevo-carotidinae infranormales: left carotid is superficial (right is lacking).
B–6a–d	Ligamentum unicarotidinae (ligamentum ottleyi): entire, right side.
B–6a–s	Ligamentum unicarotidinae (ligamentum ottleyi): entire, left side.
B–6b–d	Ligamentum unicarotidinae: incomplete or lacking, right side.
B–6b–s	Ligamentum unicarotidinae: incomplete or lacking, left side.

By means of this codified classification, all birds can be placed in one of two major groups with respect to the adult carotid arrangement, and these in turn may then be further subdivided to show their apparent value with respect to levels of evolution and possible phyletic relationships. Furthermore, this carotid classification may be used to show both species evolution and, ontogenetically, the course of changes which took place during embryonic development.

This scheme has the advantage of being able to show where large (macro) or small (micro) steps in avian evolution of the aortic arch system has taken place. It also has the particular advantage of demonstrating the probable ontogenetic course of events which took place within any single or individual specimen.

Arterial arrangement-patterns in neck and thorax

Class AVES

Basically bicarotid. Several functional and structural modifications are found in both families and orders.

As in other amniotes, the carotid, systemic, and pulmonary arches alone remain as functional derivatives of the embryonic aortic arches. The left ligamentum botalli atrophies and may become incorporated into the ligamentum aortae or it may be completely resorbed. The right ligamentum botalli may remain as a persistent vestige of the ductus botalli or it may be reduced to a ligamentous "button"; it may be incorporated into the wall of the right radix aortae or be completely resorbed.

The right systemic arch alone remains as the functional vessel carrying blood from the aortic root to the functional radix aortae. Biswas (1946) has reported the occurrence of both a left and right systemic arch in a specimen of *Ploceus philippinus philippinus*, along with a patent left radix aortae which was occluded at the posterior end. A left ligamentum botalli was present in this specimen.

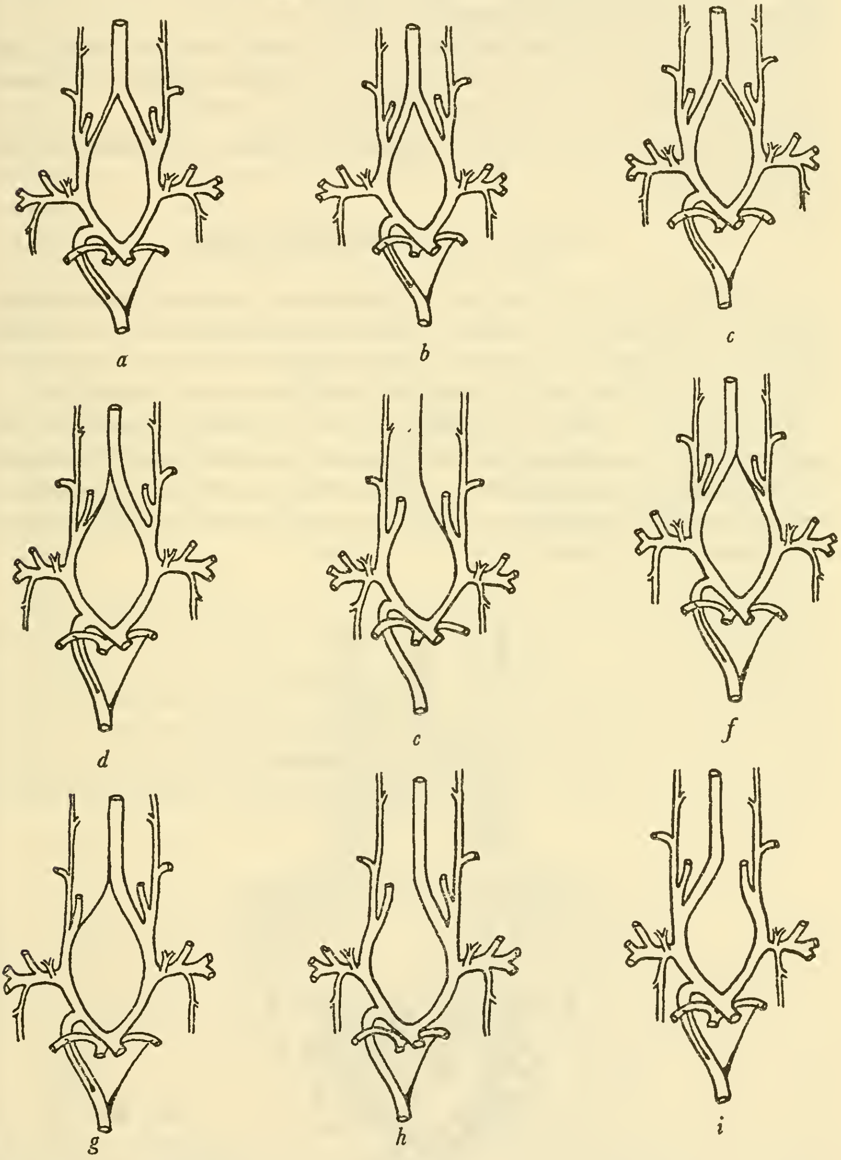

FIGURE 112.—Arrangements of the dorsal carotid arteries and the associated cervical and thoracic arteries in Aves Unicarotidinae (ventral views). Types (for code see pp. 546, 548–549): *a*, B–2–d; *b*, B–1; *c*, B–2–s; *d*, B–3a–d; *e*, B–6–s; *f*, B–3a–s; *g*, B–3b–d; *h*, B–4–s; *i*, B–4–d.

The left radix aortae usually persists throughout most of its length as a ligamentum aortae.

The ducti carotici are usually functionally modified, although the right ductus caroticus frequently is found as a persistent ductus in several species of birds, and may be expected to occur in any species of bird as an anomaly (Bhaduri, 1939; Finn, 1891; Glenny, 1940b, 1944a; Mathew, 1944; Subhapradha, 1944).

The anterior dorsal radices aortae or dorsal carotids usually lie within the hypapophysial canal, although exceptions to this have been reported (Beddard, 1898; Garrod, 1873; Glenny, 1954b).

Modifications of the dorsal carotids have been discussed in the previous chapter.

Subclass ARCHAEORNITHES

Ancestral birds, which are as yet unknown, were in all probability bicarotid. In the short-necked forms these vessels may have been superficial, although it is more than probable that they entered the hypapophysial canal as is the case in the alligator and crocodile.

The relatively close relationship to the crocodilians seems to be confirmed by the arrangement of the cervical and thoracic arteries in both birds and the alligator. The latter presents a laevo-carotidinae normales arrangement, with the single dorsal carotid entering the hypapophysial canal.

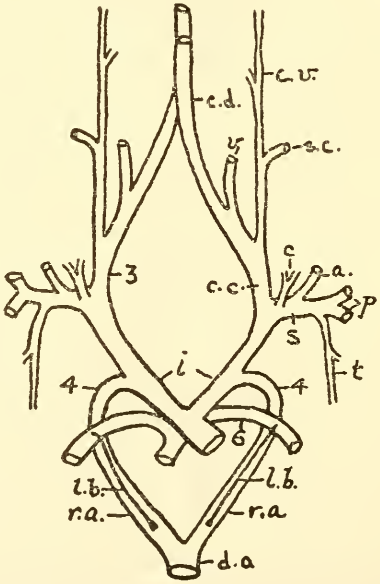

Figure 113.—Main cervical and thoracic arteries as postulated for the Archaeornithes, ventral view. (For explanation of symbols see facing page.)

It is possible that the left systemic arch arose at the base of the left innominate artery and continued to function as in reptiles. In some forms, the left systemic arch may have become somewhat reduced. Both ducti botalli were probably reduced to ligamentous vestiges, although either may have presented a lumen from time to time.

The subclavian, pectoral stem, and branches were possibly variable, but essentially similar to those of most present-day orders of birds. The vertebrals and superficial cervicals either had a common root or arose separately but in the same general location, near the thyroid gland.

The ventral carotids probably maintained their anterior cephalic connections. The condition of uniform bilaterality probably persisted in most of the earliest forms. It is possible that in these early avian ancestral forms there may have been reduction in diameter of both the left systemic arch and the left radix aortae.

The ventricle was probably completely divided into left and right chambers, and the pulmonary root emerged from the right ventricle while the aortic root emerged from the left ventricle. One essential difference exists between the crocodilian heart and the avian heart—that is, the left systemic arch probably arose from the aortic root or from the innominate artery instead of having a separate root arising or emerging from the right ventricle as in the crocodilian heart.

Subclass NEORNITHES

Most of the ancestral forms were probably bicarotid, although some may have been undergoing evolutionary changes toward the unicarotid condition. For the most part, there probably was a great similarity in the aortic arch system of the early Neornithes to that of the true avian archaeornithial ancestors. Certain advances resulting from both structural and functional modifications, including atrophy and deletion of parts, undoubtedly took place. Among these early modi-

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EXPLANATION OF SYMBOLS ON FIGURES 113–118

3.	Third aortic (carotid) arch.	d.c.	Ductus caroticus.
4.	Fourth aortic (systemic) arch.	d.s.	Ductus shawi.
6.	Sixth aortic (pulmonary) arch.	g.	Arteria gallinae (supplies trachea).
4x.	Functional ductus caroticus serving as the right fourth aortic (systemic) arch.	i.	Innominate arteries.
		l.a.	Ligamentum aortae.
		l.b.	Ligamentum botalli.
a.	Axillary artery.	oe.	Oesophageal arteries.
c.	Coracoid artery.	p.	Pectoral arteries.
c.c.	Common carotid artery.	r.a.	Radix (radices) aortae.
c.d.	Dorsal carotid artery.	s.	Subclavian artery.
c.v.	Ventral carotid or superficial cervical artery.	s.c.	Subscapular artery.
		t.	Thoracic or intercostal artery.
d.a.	Dorsal (abdominal) aorta.	v.	Vertebral artery.

fications was the loss of the left systemic arch with the reduction to a ligament of the left radix aortae. This may have been accompanied by further atrophy and reduction in the vestiges of the ducti botalli. The site of junction of the vertebrals with the carotids probably underwent considerable change with the result that there was considerable variation within the several major groups of birds.

For the most part, the bicarotid condition persisted in most of the major groups of birds. But, as evolution of the aortic arch system progressed, there was considerable variation in the arrangement of the dorsal carotids. During the process both left and right configurations probably arose, but the widespread occurrence of the bicarotid and laevocarotid conditions may have led to the present dominance of these two main arrangement-patterns.

Evidence that this process is continuing may be found in several families of extant birds, noted below.

Order STRUTHIONIFORMES

Family Struthionidae

Carotids A–1; type A coracoid artery; type 1 thoracic artery; ligamentum aortae and ligamentum botalli prominent; vertebrals and superficial cervicals arise from the common carotids either separately or from a common root.

Garrod (1873) reported *Struthio camelus* to be bicarotidinae normales.

References: Fleming, 1926; Garrod, 1873.

Species studied

By Garrod	By Glenny
Struthio camelus Linné	*Struthio camelus australis* Gurney

Order RHEIFORMES

Family Rheidae

Carotids B–4–s; type A coracoid artery; type 1 thoracic artery; ligamentum aortae and ligamentum botalli present; vertebrals and superficial cervicals arise from the common carotids separately but in close association with each other.

F. P. Evans (1883) stated that the right carotid is evidently present, though much smaller than the left and instead of converging to meet the left, which enters the hypapophysial canal, it continues onwards as a superficial vessel in close association with the right vagus nerve and jugular vein.

Glenny (1943d) observed much the same condition in a rhea embryo, but difficulty in dissection made it impossible to follow the superficial vessel to the head. Further studies are necessary to make clear the relationships of these vessels in the rheas.

References: F. P. Evans, 1883; Garrod, 1873; Glenny, 1943d.

Species studied

By Evans	By Glenny
Rhea americana (Linné)	*Rhea americana intermedia* Rothschild and Chubb
By Garrod	
Rhea americana (Linné)	

Order CASUARIIFORMES

Family Casuariidae

Carotids typically A–1, but may vary; type A coracoid artery; type 1 thoracic artery; vertebrals and superficial cervicals are variable in origin from the common carotid arteries.

Garrod reported two species of *Casuarius* to be bicarotidinae normales (A–1). In a dissection of a zoo specimen of *Casuarius*, I found that the left dorsal carotid alone entered the hypapophysial canal (B–4–s).

It is possible that in the course of evolution of these birds some specific or subspecific variation in the carotid arteries may have taken place. It might be quite profitable to make an extensive study of the arteries in the different species and subspecies of the cassowaries and to correlate these findings with their geographical distribution.

References: Garrod, 1873; Glenny, 1942c.

Species studied

By Garrod	By Glenny
Casuarius bicarunculatus P. L. Sclater	*Casuarius* sp. (zoo specimen)
Casuarius bennetti Gould	

Family Dromiceiidae

Carotids A–1; no other details available.

Species studied

By Garrod

Dromiceius n.-hollandiae (Latham)

Order APTERYGIFORMES

Family Apterygidae

Carotids B–4–s; coracoid artery arises from the subclavian medial to the thoracic artery; no axillary artery could be observed; ligamentum aortae and ligamentum botalli both present; pectoral branches greatly modified, and somewhat similar to those observed in *Casuarius* sp.; vertebrals and superficial cervicals arise variously and independent of each other from the common carotids; thyroids arise from the innominate arteries near the base of the common carotid arteries.

Further study of the thoracic and cervical arteries of the kiwis should be carried out in an effort to obtain as much information as possible about these birds.

References: Garrod, 1873; Glenny, 1942b; Owen, 1841.

SPECIES STUDIED

By Garrod

Apteryx australis mantelli Bartlett
Apteryx owenii Gould

By Glenny

Apteryx australis mantelli Bartlett

By Owen

Apteryx australis Shaw

Order TINAMIFORMES

Family TINAMIDAE

Carotids A–1; type A coracoid artery; type 1 to type 4 thoracic artery; both the ligamentum aortae and the ligamentum botalli are usually present; vertebrals and superficial cervicals arise variously from the common carotid, either separately or from a common root. Considerable variability in the secondary arteries of the neck and thorax exists.

References: Garrod, 1873; Glenny, 1946a.

SPECIES STUDIED

By Garrod

Crypturus sallaei=*Crypturellus cinnamomeus goldmani* (Nelson)
Rhynchotus rufescens (Temminck)

By Glenny

Tinamus major (Gmelin)
Crypturellus sp.
Crypturellus cinnamomeus (Lesson)
Nothoprocta perdicaria (Kittlitz)
Nothura maculosa boliviana Salvadori
Eudromia elegans d'Orbigny and Geoffroy, (2)

Order SPHENISCIFORMES

Family SPHENISCIDAE

Carotids A–1; type A coracoid artery; type 1 thoracic artery; ligamentum aortae present and prominent; ligamentum botalli usually present; vertebrals arise variously from the common carotids, but usually not in common with the superficial cervical arteries.

References: Garrod, 1873; Glenny, 1944c, 1947a; Jullien, 1878; Müller, 1908.

Species studied

By Garrod

Aptenodytes pennantii=*Aptenodytes patagonica* J. F. Miller
Spheniscus demersus (Linné)
Spheniscus humboldti Meyen

By Glenny

Aptenodytes forsteri G. R. Gray
Pygoscelis papua (Forster)
Eudyptes crestatus (J. F. Miller)
Spheniscus demersus (Linné) (2)
Spheniscus humboldti Meyen
Spheniscus mendiculus Sundevall

By Jullien

Aptenodytes patagonica J. F. Miller

Order GAVIIFORMES

Family Gaviidae

Carotids A–1; type A coracoid artery; type 1 thoracic artery; ligamentum aortae and ligamentum botalli present; vertebrals and superficial cervicals arise separately from the common carotids; oesophageal arteries variable in number and site of origin.

References: Garrod, 1873; Glenny, 1945e.

Species studied

By Garrod

Colymbus glacialis=*Gavia immer* (Brünnich)

By Glenny

Gavia stellata (Pontoppidan) (2)
Gavia immer (Brünnich) (2)

Order COLYMBIFORMES

Family Colymbidae

Carotids B–4–s; type A and type E coracoid arteries; type 1 to type 4 thoracic arteries; ligamentum aortae present; ligamentum botalli may be present or lacking; vertebrals and superficial cervicals arise variously from the common carotid; oesophageal blood supply highly variable and in some species extensive.

References: Garrod, 1873; Glenny, 1946b.

Species studied

By Garrod

Podiceps minor=*Poliocephalus ruficollis* (Pallas)
Podiceps cristatus=*Colymbus cristatus* Linné

By Glenny

Colymbus chilensis (Lesson)
Colymbus occipitalis (Garnot)
Colymbus auritus Linné (2)
Colymbus nigricollis californicus (Heermann)
Colymbus grisegena holböllii (Rheinhardt)
Aechmorphorus major (Boddaert)
Podilymbus podiceps podiceps (Linné) (2)

Order PROCELLARIIFORMES

Typically bicarotid (A–1) or rarely unicarotid; type A coracoid artery; type 1 thoracic artery; ligamentum aortae present, but sometimes much reduced; ligamentum botalli frequently present; vertebrals and superficial cervicals variable in origin from the common carotid arteries.

Reference: Garrod, 1873.

Family Diomedeidae

Right ligamentum botalli present.

Species studied

By Glenny

Diomedea immutabilis Rothschild

Family Procellariidae

Subfamily Fulmarinae

Ligamentum botalli usually present (reduced or lacking in *Pachyptila desolata*); vertebrals arise separately from the carotid at or near the base of the cervicals.

Subfamily Puffininae

Ligamentum botalli usually present (reduced or lacking in *Bulweria bulweria*, *Pterodroma lessonii*, *Puffinus lherminieri subalaris*); origin of vertebrals highly variable.

Priocella antarctica (USNM 321474), carotids: B–3a–d.

Species studied

By Garrod

Prion vittata=*Pachyptila forsteri* (Latham)
Aestrelata lessoni=*Pterodroma lessonii* (Garnot)
Thalassidroma bulweri=*Bulweria bulwerii* (Jardine & Selby)

By Glenny

Daption capensis (Linné)
Fulmarus glacialis (Linné) (2)
Halobaena caerulea (Gmelin)
Pachyptila desolata (Gmelin) (2)
Priocella antarctica (Stephens)
Procellaria aequinoctialis Linné
Puffinus griseus (Gmelin)
Puffinus nativitatis Streets
Puffinus opisthomelas Coues
Puffinus lherminieri subalaris Ridgway
Pterodroma lessonii (Garnot)
Pterodroma leucoptera hypoleuca (Salvin) (2)
Bulweria bulwerii (Jardine and Selby)

Family Hydrobatidae

Ligamentum aortae usually reduced; ligamentum botalli usually lacking, or when present only as a linea botalli; superficial cervical arteries variable in number but more are present in *Oceanodroma* than in other genera studied.

SPECIES STUDIED

By Garrod

Thalassidroma pelagica=*Hydrobates pelagicus* (Linné)
Thalassidroma fregata=*Pelagodroma marina* (Latham)

By Glenny

Oceanites oceanicus (Kuhl)
Oceanites gracilis galapagoensis Lowe
Oceanodroma leucorhoa (Vieillot)
Oceanodroma macrodactyla W. E. Bryant
Oceanodroma monorhis socorroensis C. H. Townsend
Oceanodroma hornbyi (G. R. Gray)
Halocyptena microsoma Coues

Family PELECANOIDIDAE

Ligamentum aortae prominent; ligamentum botalli lacking or reduced to a linea botalli; vertebrals and cervicals usually arise separately from the common carotid; superficial cervicals variable, but usually two pairs are present.

In *Pelecanoides exsul* the ligamentum aortae may present a lumen for a short distance. The left dorsal carotid alone enters the hypapophysial canal in *Pelecanoides garnotii* (USNM 344806): B–4–s.

SPECIES STUDIED

By Glenny

Pelecanoides exsul Salvin (2)
Pelecanoides garnotii (Lesson)

Order PELECANIFORMES

Both bicarotid and unicarotid arrangements occur within the order; type A coracoid artery; type 1 thoracic artery except in *Morus bassanus* (type 2 or type 3); ligamentum aortae present; ligamentum botalli either present or absent; origin of vertebrals and superficial cervicals variable.

Reference: Garrod, 1873.

Family PHAËTHONTIDAE

Carotids A–1; presence of ligamentum botalli variable.

SPECIES STUDIED

By Glenny

Phaëthon lepturus dorotheae Mathews
Phaëthon rubricauda rothschildi (Mathews)

By Garrod

Phaëthon sp.

Family PELECANIDAE

Carotids B–3b–d; ligamentum botalli generally present.

The unicarotid condition in this family is clearly a further step in the modification of the conjugate carotid condition of the dorsal carotid arteries.

Species studied

By Glenny

Pelecanus erythrorhynchos Gmelin
Pelecanus occidentalis carolinensis Gmelin

Family Sulidae

Carotids B–4–s (*Sula* spp.) and A–1 (*Morus bassanus*); type 1 thoracic artery (*Sula* spp.) and type 2 or type 3 thoracic artery (*Morus bassanus*); ligamentum botalli lacking.

Species studied

By Garrod

Sula bassana=*Morus bassanus* (Linné)

By Glenny

Morus bassanus (Linné)
Sula sula sula (Linné)
Sula dactylatra personata Gould
Sula leucogaster etesiaca Thayer and Bangs
Sula leucogaster plotus (Forster)

Family Phalacrocoracidae

Carotids A–1; ligamentum botalli lacking; vertebrals and superficial cervicals usually have separate points of origin from the common carotid arteries.

Species studied

By Glenny

Phalacrocorax auritus floridanus (Audubon)
Phalacrocorax pelagicus pelagicus Pallas
Phalacrocorax urile (Gmelin)
Phalacrocorax verrucosus (Cabanis)

By Garrod

Phalacrocorax carbo (Linné)

Family Anhingidae

Carotids B–4–s; ligamentum botalli is reduced to a linea botalli.

Species studied

By Glenny

Anhinga anhinga (Linné)

Family Fregatidae

Carotids A–1 and B–4–s; ligamentum botalli absent.

Garrod (1873) reported the bicarotid condition in *Fregata aquila*, while I found the laevocarotid condition in *Fregata minor palmerstoni*.

Species studied

By Garrod

Fregata aquila Linné

By Glenny

Fregata minor palmerstoni (Gmelin)

Order CICONIIFORMES

The arrangement of the dorsal carotids is highly variable, but basically bicarotid (see list of species studied); type A coracoid artery;

type 1 thoracic artery; ligamentum aortae present; presence of the ligamentum botalli variable; vertebrals and superficial cervicals usually arise separately from the common carotids.

This order appears to be in a state of flux insofar as evolution of the aortic arch system is concerned. This evolution is not restricted to a single family, although the greatest evidence of carotid evolution is to be observed in the Ardeidae. It has been found that, even within the same species, both the bicarotid and conjugate carotid conditions may occur, and that within a species which is normally conjugate carotid, both the B–1 and the B–2 condition may exist. It may be presumed, therefore, that further variation in the carotids may take place, and that any apparent deviation in a condition as reported may be accounted for on the basis of individual levels in the evolution of this system.

References: Finn, 1891; Garrod, 1873; Glenny, 1940a, 1945c, 1953a.

Family ARDEIDAE

Carotids variable; presence of the ligamentum botalli variable.

The high degree of variation in the dorsal carotids of this family seems to indicate that these birds are undergoing further speciation, at least with respect to the aortic arch system.

SPECIES STUDIED

By Finn

Nycticorax violaceus=*Nyctanassa violacea* (Linné) (A–1)

By Garrod

Ardea goliath Cretzschmar (A–1)
Ardea cinerea Linné (A–1)
Ardea purpurea Linné (A–1)
Ardea alba=*Casmerodius albus albus* (Linné) (A–1)
Ardea egretta=*Casmerodius albus egretta* (Gmelin) (A–1)
Ardea garzetta=*Egretta garzetta* (Linné) (A–1)
Ardea candidissima=*Leucophoyx thula* (Molina) (A–1)
Nycticorax europaeus=*Nycticorax nycticorax* (Linné) (A–1)
Botaurus stellaris (Linné) (B–1)

By Glenny

Ardea herodias treganzai Court (B–1)
Ardea herodias herodias Linné (A–1)
Butorides virescens virescens (Linné) (B–1)
Butorides sundevalli Reichenow (A–1)
Florida caerulea (Linné) (A–1)
Ardeola speciosa (Horsfield) (B–2–s)
Bubulcus ibis ibis (Linné) (A–1)
Bubulcus ibis coromandus (Boddaert) (A–1)
Dichromanassa rufescens (Gmelin) (A–1)
Casmerodius albus albus (Linné) (A–1)
Leucophoyx thula brewsteri (Thayer and Bangs) (B–1)
Hydranassa tricolor ruficollis (Gosse) (A–1)
Nyctanassa violacea pauper (Sclater and Salvin) (A–1)
Ixobrychus minutus minutus (Linné) (A–1)
Ixobrychus sinensis sinensis (Gmelin) (B–1)
Ixobrychus sinensis bryani (Seale) (A–1)
Botaurus lentiginosus (Montagu) (2) (B–1 and B–2–s)

Family Cochleariidae

Carotids A–1; ligamentum botalli reduced to a linea botalli.

Species studied

By Glenny

Cochlearius cochlearius zeledoni (Ridgway) (A–1)

Family Balaenicipitidae

Carotids B–4–s; the right dorsal carotid appears to have become functionally modified as a superficial cervical artery (comes nervi vagi), and to have lost its anterior connection with the carotids of the head region; a pair of arteries which arise from the innominate arteries near the base of the subclavian arteries supply the oesophagus.

Species studied

By Glenny

Balaeniceps rex Gould (B–4–s)

Family Scopidae

No information is available for this family of birds.

Family Ciconiidae

Carotids A–1; ligamentum botalli reduced to a linea botalli.

Species studied

By Garrod

Ciconia alba=*Ciconia ciconia* (Linné) (A–1)
Ciconia nigra (Linné) (A–1)
Leptoptilos crumeniferus (Lesson) (A–1)

By Glenny

Ciconia ciconia (Linné) (A–1)

Family Threskiornithidae

Carotids A–1; ligamentum botalli present, at least in part.

Species studied

By Garrod

Ibis melanocephala=*Threskiornis melanocephala* (Latham) (A–1)
Ibis strictipennis=*Threskiornis molucca strictipennis* (Gould) (A–1)
Ibis nippon=*Nipponia nippon* (Temminck) (A–1)
Ibis rubra=*Guara rubra* (Linné) (A–1)
Platalea leucorodia Linné (A–1)

By Glenny

Guara alba (Linné) (A–1)
Plegadis guarauna (Linné) (A–1)

Family Phoenicopteridae

Carotids B–2–s; ligamentum botalli present; vertebrals arise from the common carotids posterior to the origin of the superficial cervicals.

Species studied

By Garrod	By Glenny
Phoenicopterus antiquorum Temminck (B–2–s)	*Phoenicopterus ruber* Linné (B–2–s)
Phoenicopterus ruber Linné (B–2–s)	

ORDER ANSERIFORMES

Typically bicarotid (A–1); ligamentum aortae present; ligamentum botalli rarely reduced or absent; types A and E coracoid arteries; type 1 thoracic artery; vertebrals and superficial cervicals highly variable in points of origin, with considerable variation within a species—not a stable pattern in the Anatidae, and evolution of the cervical arteries appears to be undergoing considerable and wide deviation; a complex oesophageal supply is usually encountered. Occurrence of a patent ductus caroticus in *Anas spinicauda* was reported by Finn (1891).

There are no apparent significant or characteristic differences in the basic arterial patterns of the Anhimidae and Anatidae, aside from the several minor differences which are found to occur within the Anatidae.

In the Anhimidae, the vertebrals appear to arise independently from the common carotid, while the vertebrals and superficial cervicals, in the Anatidae, generally have a short, common root arising from the common carotid artery.

References: Bauer, 1825; Finn, 1891; Garrod, 1873; Glenny, 1944d; Hahn, 1830; Rabl, 1906a.

Family Anhimidae

Carotids A–1; ligamentum botalli prominent.

Species studied

By Glenny

Chauna torquata (Oken)

Family Anatidae

Carotids A–1; ligamentum botalli usually present; superficial cervical arteries variable in number and points of origin.

Species studied

By Finn

Dafila spinicauda=*Anas spinicauda* Vieillot

By Garrod

Cygnus buccinator Richardson
Cygnus nigricollis=*Cygnus melancoriphus* (Molina)
Anser segetum=*Anser fabalis* (Latham)
Bernicla canadensis=*Branta canadensis* (Linné)
Chloëphaga sp.
Dendrocygna fulva=*Dendrocygna bicolor* (Vieillot)
Dendrocygna viduata (Linné)
Dendrocygna autumnalis (Linné)
Tadorna rutila=*Casarca ferruginea* (Pallas)
Querquedula crecca=*Anas crecca* Linné
Dafila spinicauda=*Anas spinicauda* Vieillot
Mareca penelope (Linné)
Aix galericulata=*Dendronessa galericulata* (Linné)
Metopiana peposaca (Vieillot)
Fuligula cristata=*Nyroca fuligula* (Linné)
Mergus albellus=*Mergellus albellus* (Linné)
Mergus castor=*Mergus serrator* Linné

By Glenny

Cygnus columbianus (Ord) (2)
Cygnus olor (Gmelin)
Chen caerulescens (Linné)
Chen atlantica Kennard
Anser albifrons albifrons (Scopoli)
Branta canadensis canadensis (Linné)
Branta canadensis leucopareia Brandt
Alpochen aegyptiaca (Linné)
Coscoroba coscoroba (Molina)
Nyroca collaris (Donovan) (2)
Nyroca marila nearctica (Stejneger)
Bucephala clangula americana (Bonaparte)
Bucephala albeola (Linné)
Clangula hyemalis (Linné) (2)
Oidemia nigra americana Swainson
Melanitta fusca deglandi (Bonaparte) (3)
Melanitta perspicillata (Linné) (2)
Mergus merganser americanus Cassin
Mergus serrator Linné (3)

Order FALCONIFORMES

Carotids A–1; type A coracoid artery; type 1 thoracic artery; ligamentum aortae present; ligamentum botalli usually present, but may be reduced in length or more rarely remain as a linea botalli; vertebrals and superficial cervicals usually arise separately—the latter posterior to the vertebrals, but in some instances these vessels may have a common root from the common carotid artery.

References: Bauer, 1825; Beddard, 1898; Garrod, 1873; Glenny, 1941a.

Family CATHARTIDAE

Species studied

By Garrod

Cathartes atratus=*Coragyps atratus* (Bechstein)
Gyparchus papa=*Sarcoramphus papa* (Linné)

By Glenny

Gymnogyps californianus (Shaw)
Cathartes aura septentrionalis Wied

Family SAGITTARIIDAE

Species studied

By Garrod

Sepentarius reptilivorus=*Sagittarius serpentarius* (J. F. Miller)

Family ACCIPITRIDAE

SPECIES STUDIED

By Beddard

Spizaëtus sp.

By Garrod

Milvus ictinus=*Milvus milvus* (Linné)
Astur palumbarius=*Accipter gentilis* (Linné)
Buteo vulgaris=*Buteo buteo* (Linné)
Archibuteo lagopus=*Buteo lagopus* (Pontoppidan)
Meliërax monogrammicus=*Kaupifalco monogrammicus* (Temminck)
Thrasaëtus harpyia=*Harpia harpyja* (Linné)
Aquila audax=*Uroaëtus audax* (Latham)
Haliaeetus vocifer (Daudin)
Haliaeetus albicilla (Linne)
Aquila naevioïdes=*Aquila rapax* (Temminck)
Gyps fulvus (Hablizl)
Neophron percnopterus (Linné)
Circus cineraceus=*Circus cinereus* Vieillot
Helotarsus ecaudatus=*Terathopius ecaudatus* (Daudin)
Spilornis cheela (Latham)

By Glenny

Buteo jamaicensis borealis (Gmelin) (3)
Buteo lagopus s.-johannis (Gmelin) (3)
Aquila chrysaëtos (Linné) **(2)**
Necrosyrtes monachus monachus (Temminck)
Circus cyaneus hudsonius (Linné)

By Hochstetter

Aquila naevia=*Aquila pomarina* C. L. Brehm
Circus cineraceus=*Circus cinereus* Vieillot

FAMILY PANDIOINDAE

SPECIES STUDIED

By Glenny

Pandion haliaetus carolinensis (Gmelin)

Family FALCONIDAE

SPECIES STUDIED

By Garrod

Polyborus braziliensis=*Polyborus plancus braziliensis* (Gmelin)
Falco peregrinus Tunstall
Falco melanogenys=*Falco peregrinus macropus* Swainson
Hypotriorchis subbuteo=*Falco subbuteo* Linné
Tinnunculus alaudarius=*Falco moluccensis* (Bonaparte)

By Glenny

Falco sparvarius sparvarius Linné

Order GALLIFORMES

Carotids A-1, except for the Megapodidae which are unicarotid; origin of the coracoid and thoracic arteries varies within the order and within the families; ligamentum aortae present; ligamentum botalli usually present, but may be absent in many of the Megapodidae; vertebrals and superficial cervicals usually have a common root from the common carotid artery.

References: Bakst and Chafee, 1928; Balfour, 1873; Barkow, 1843; Beddard, 1898; Bremer, 1928; Buell, 1922; H. Evans, 1909a, 1909b; Fleming, 1926; Garrod, 1873; Glenny, 1951a; H. Hahn, 1909; Hughes, 1934; Kashchenko, 1887; Krassnig, 1913a; Lillie, 1908, 1919; Locy, 1906; Mackay, 1887; Mall, 1887; Patten, 1929; Pohlman, 1920; Quiring, 1933; C. G. Sabin, 1905; F. R. Sabin, 1917; Squier, 1916; Tonge, 1869; Twining, 1906; Vialleton, 1892.

Family MEGAPODIIDAE

Unicarotid (see list of species below); coracoid artery usually type A, but if more than one pair is present one may be opposite or lateral to the axillary artery (type D); type 1 thoracic artery; ligamentum botalli greatly reduced or absent.

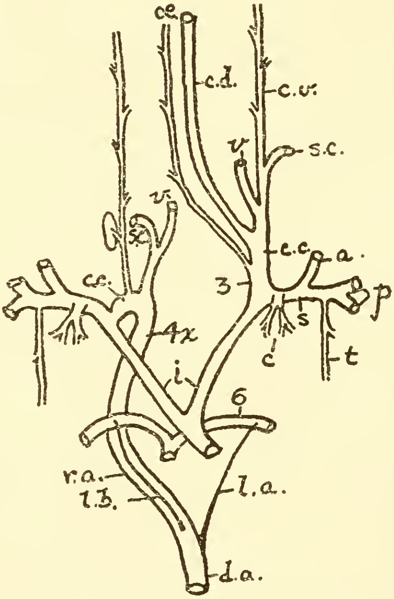

FIGURE 114.—Main cervical and thoracic arteries in *Megapodius freycinet layardi*, ventral view. (For explanation of symbols see p. 551.)

In a single specimen of *Megapodius layardi* (AMNH specimen), the right systemic arch was absent, the ductus caroticus serving to carry the blood from the carotid arch to the right radix aortae (fig. 114). While this is the first such instance to be reported, it may well be found to occur in other species.

SPECIES STUDIED

By Garrod

Talegalla lathami=*Alectura lathami* J. E. Gray (B–4–s)

Megacephalon maleo=*Macrocephalon maleo* S. Müller (B–4–s)

By Glenny

Megapodius sp. (B–4–s)

Megapodius nicobariensis Blyth (B–2–s)

Megapodius eremita eremita Hartlaub (2) (B–4–s)

Megapodius layardi Tristram (B–4–s)

Megapodius pritchardii G. R. Gray (2) (B–3b–d)

Family CRACIDAE

Carotids A–1; types 1, 2, and 4 thoracic artery; ligamentum botalli persistent; the arteria ventralis gallinae is present and arises variously from the base of the subclavian artery or from the common carotid artery.

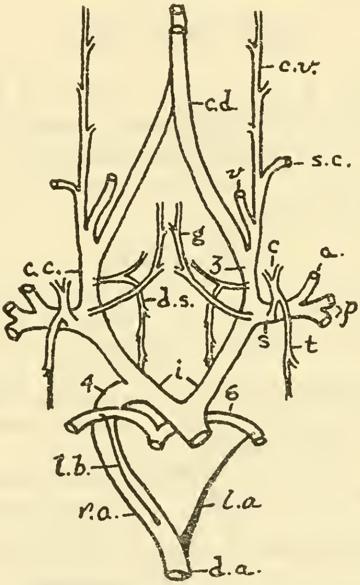

FIGURE 115.—Main cervical and thoracic arteries in *Penelope argyrotis argyrotis*, ventral view. (For explanation of symbols see p. 551.)

SPECIES STUDIED

By Garrod

Crax incommoda=*Crax pinima* Pelzeln

Crax globicera=*Crax rubra* Linné

Penelope cristatus=*Penelope purpurascens aequatorialis* Salvadori and Festa

Ortalida albiventris=*Ortalis araucuan* (Spix)

By Glenny

Crax sp.=? *Crax nigra* Linné

Pipile cumanensis (Jacquin)

Penelope argyrotis argyrotis (Bonaparte)

Family TETRAONIDAE

Carotids A–1; type A coracoid artery; type 1 thoracic artery; ligamentum botalli usually much reduced or lacking; vertebrals and superficial cervicals have a common root from the common carotid artery; arteria ventralis gallinae arises variously from the subclavian or common carotid.

SPECIES STUDIED

By Garrod

Tetrao urogallus Linné
Tetrao tetrix=*Lyrurus tetrix* (Linné)

By Glenny

Lagopus lagopus (Linné)
Lagopus lagopus alleni Stejneger
Lagopus mutus hyperboreus Sundevall
Bonasa umbellus umbellus (Linné) (3)
Tympanuchus cupido cupido (Linné)
Tympanuchus cupido pinnatus (Brewster)

Family PHASIANIDAE

Carotids A–1; type A and type D coracoid arteries; type 1 to type 4 thoracic artery; ligamentum botalli usually present; vertebrals and superficial cervicals generally have a common root arising from the common carotid artery; the arteria ventralis gallinae arises as a branch of the subclavian artery.

SPECIES STUDIED

By Garrod

Ortyx virginianus=*Colinus virginianus* (Linné)
Eupsychortyx cristatus=*Colinus cristatus* (Linné)
Odontophorus dentatus=*Odontophorus capueira* (Spix)
Caccabis chukar=*Alectoris graeca chukar* (J. E. Gray)
Francolinus vulgaris=*Francolinus francolinus* (Linné)
Francolinus gularis (Temminck)
Francolinus pondicerianus (Gmelin)
Francolinus clappertoni Children
Francolinus afer=*Pternistis afer* (P. L. S. Müller)
Perdix cinerea=*Perdix perdix* (Linné)
Coturnix communis=*Coturnix coturnix* (Linné)
Arboricola torqueola=*Arborophila torqueola* (Valenciennes)
Rollulus coronatus=*Rollulus rouloul* (Scopoli)
Ceriornis temminckii=*Tragopan temminckii* (J. E. Gray)
Euplocamus albo-cristatus=*Gennaeus leucomelanos hamiltonii* (J. E. Gray)
Euplocamus horsfieldii=*Gennaeus horsfieldii* (G. R. Gray)
Euplocamus vieilloti=*Lophura rufa* (Raffles)
Euplocamus pyronotus=*Houppifer erythrophthalmus pyronotus* (G. R. Gray)
Euplocamus erythrophthalmus=*Houppifer erythrophthalmus pyronotus* (G. R. Gray)
Gallus bankiva=*Gallus gallus bankiva* Temminck
Phasianus colchicus Linné
Phasianus versicolor=*Phasianus colchicus versicolor* Vieillot
Phasianus reevesii=*Syrmaticus reevesii* (J. E. Gray)
Thaumalia picta=*Chrysolophus pictus* (Linné)
Thaumalia amherstiae=*Chrysolophus amherstiae* (Leadbeater)
Argus giganteus=*Argusianus argus argus* (Linné)
Pavo nigripennis=*Pavo cristatus* Linné (melanistic phase)
Pavo muticus Linné

By Glenny

Oreortyx picta (Douglas)
Lophortyx californica (Shaw)
Colinus virginianus (Linné)
Colinus virginianus cubanensis (G. R. Gray)
Odontophorus columbianus (Gould)
Alectoris graeca chukar (J. E. Gray)
Arborophila brunneopectus henrici (Oustalet)
Crossoptilon mantchuricum Swinhoe
Gallus gallus domesticus Darwin
Catreus wallichii (Hardwicke)
Phasianus colchicus torquatus Gmelin
Chrysolophus pictus (Linné)
Pavo cristatus Linné (white phase)

Family NUMIDIDAE

Carotids A-1; type B coracoid artery; type 1 thoracic artery; ligamentum botalli much reduced; vertebrals and superficial cervicals have a common root from the common carotid; the arteria ventralis gallinae arises from the base of the subclavian artery.

SPECIES STUDIED

By Garrod	By Glenny
Numida meleagris (Linné)	*Numida meleagris* (Linné)

Family MELEAGRIDIDAE

Carotids A-1; type A or type B coracoid artery; type 1 thoracic artery; ligamentum botalli much reduced; vertebrals and cervicals have a common root from the common carotid; the arteria ventralis gallinae arises as a branch from the base of the subclavian artery.

SPECIES STUDIED

By Garrod	By Glenny
Meleagris gallopavo Linné	*Meleagris gallopavo* Linné

Family OPISTHOCOMIDAE

Carotids A-1; type 2 thoracic artery; coracoid artery is medial to the thoracic artery; ligamentum botalli present; vertebrals and superficial cervicals have a common root from the common carotid artery; the arteria ventralis gallinae is absent or greatly reduced.

SPECIES STUDIED

By Glenny

Opisthocomus hoazin (P. L. S. Müller) (2)

Order GRUIFORMES

Carotids A-1 and B-4; coracoid artery usually type A, but rarely type E is present; type 1 to type 4 thoracic artery; ligamentum aortae present; ligamentum botalli may be present or absent; vertebrals and superficial cervicals arise either separately or from a common root from the common carotid arteries.

References: Beddard, 1898; Garrod, 1873; Glenny 1940a, 1945d, 1947b; Wetmore, 1951.

Family MESOENATIDAE

Carotids A–1; type 1 thoracic artery; ligamentum botalli remains as a linea botalli; vertebrals and superficial cervicals have a common root in *Monias benschi* and *Mesoenas unicolor*, but are separate in *Mesoenas variegata.*

The clavicles in these birds are reduced to a small bone, the epicleidum, and a ligamentous vestige of the corpus claviculi (class 3 clavicle) (Glenny and Friedmann, 1954).

SPECIES STUDIED

By Glenny

Mesoenas variegata (Goeffroy)
Mesoenas unicolor (Des Murs)
Monias benschi Oustalet and Grandidier

Family TURNICIDAE

Carotids B–4–s; type 1 thoracic artery; ligamentum botalli absent; vertebrals and superficial cervicals have a common root from the common carotid artery.

SPECIES STUDIED

By Garrod

Hemipodius tachydromus = *Turnix sylvatica* (Desfontaines)

By Glenny

Turnix tanki blanfordi Blyth (2)
Turnix suscitator suscitator (Gmelin)

Family PEDIONOMIDAE

Carotids A–1, according to Wetmore (1951).

Family GRUIDAE

Carotids A–1; type A and type E coracoid artery; type 1 thoracic artery; ligamentum botalli reduced to a linea botalli or absent; vertebrals and superficial cervicals arise separately from the common carotid arteries.

SPECIES STUDIED

By Glenny

Grus antigone (Linné)
Anthropoïdes paradisea (Lichtenstein)

Family ARAMIDAE

Carotids A–1; type B coracoid artery; type 1 thoracic artery; ligamentum botalli present or reduced to a linea botalli; origin of the vertebrals and superficial cervicals variable.

Species studied

By Glenny

Aramus scolopaceus pictus (F. A. A. Meyer)

Family Psophiidae

Carotids A–1; type 1 thoracic artery; type A coracoid artery; ligamentum botalli present or reduced to a linea botalli; vertebrals and superficial cervicals arise separately from the common carotid artery, but may have a common root in some instances.

Species studied

By Glenny

Psophia leucoptera Spix

Family Rallidae

Carotids A–1; types 2, 3, and 4 thoracic artery; type A coracoid artery; ligamentum botalli present or reduced in a few species, but generally lacking; vertebrals and superficial cervicals arise separately from the common carotid, or rarely from a short common root from the common carotid.

Species studied

By Garrod

Rallus aquaticus Linné
Ocydromus sylvestris=*Tricholimnas sylvestris* (Sclater)
Aramides cayennensis = *Aramides cajanea* (P. L. S. Müller)
Crex pratensis=*Crex crex* (Linné)
Porzana americana=*Porzana flaviventer* (Boddaert)
Porzana carolinensis=*Porzana carolina* (Linné)
Gallinula chloropus (Linné)
Porphyrio madagascariensis (Latham)
Porphyrio poliocephalus melanotus Temminck

By Glenny

Rallus longirostris saturatus Ridgway
Atlantisia rogersi Lowe
Tricholimnas sylvestris (Sclater)
Ortygonax rytirhynchos (Vieillot)
Cyanolimnas cerverai Barbour and Peters
Aramides cajanea (P. L. S. Müller)
Limnocorax flavirostra (Swainson)
Porzana carolina (Linné)
Porzanula palmeri Frohawk
Coturnicops noveboracensis (Gmelin)
Neocrex erythrops (Sclater)
Poliolimnas cinereus (Vieillot)
Amaurornis phoenicurus javanica (Horsfield)
Gallinula chloropus cachinnans Bangs
Porphyrula martinica (Linné) (2)
Porphyrio porphyrio (Linné)
Porphyrio poliocephalus melanotus Temminck
Fulica americana Gmelin (3)

Family Heliornithidae

No information available.

Family Rhynochetidae

Carotids A–1; type 1 thoracic artery; type A coracoid artery; ligamentum botalli complete; vertebrals and superficial cervicals arise separately from the common carotid.

SPECIES STUDIED

By Glenny

Rhynochetos jubatus J. Verreaux and Des Murs (2)

Family EURYPYGIDAE

Carotids A–1; type 1 thoracic artery; type A coracoid artery; ligamentum aortae greatly reduced; ligamentum botalli absent; vertebrals and superficial cervicals arise separately from the common carotid artery.

SPECIES STUDIED

By Glenny

Eurypyga helias helias (Pallas)

Family CARIAMIDAE

Carotids A–1; type 1 thoracic artery; type A coracoid artery; ligamentum botalli absent or reduced to a linea botalli; vertebrals and superficial cervicals arise separately from the common carotid artery.

SPECIES STUDIED

By Glenny	By Garrod
Chunga burmeisteri (Hartlaub) *Cariama cristata* (Linné)	*Cariama cristata* (Linné)

Family OTIDAE

Information incomplete. Garrod (1873) notes the A–1 condition in *Houbara macqueeni*, while Beddard (1898) reports that two species of *Eupodotis* are B–4–d.

Presence of the ligamentum botalli may vary; the thoracic artery is probably type 1, and the vertebrals and superficial cervicals probably have separate points of origin from the common carotid arteries.

SPECIES STUDIED

By Garrod	By Beddard
Houbara macqueeni=*Chlamydotis undulata macqueenii* (J. E. Gray) (A–1)	*Eupodotis* spp. (2) (B–4–d)

Order CHARADRIIFORMES

Carotids A–1, except in two species of the Alcidae; type A coracoid artery; type 1 thoracic artery, except for type 2 in *Phalaropus fulicarius* and type 3 in *Jacana spinosa intermedia;* ligamentum aortae present; ligamentum botalli variable in presence and degree of reduction; vertebrals and superficial cervicals vary in points of origin from the common carotid arteries.

References: Beddard, 1898; Garrod, 1873; Glenny, 1947c, 1948, 1952a, 1952b; Hafferl, 1921.

Family JACANIDAE

Ligamentum botalli reduced to a linea botalli or may be entirely lacking; vertebrals and cervicals generally arise separately from the common carotid; an accessory oesophageal artery arises as a branch of the left common carotid artery.

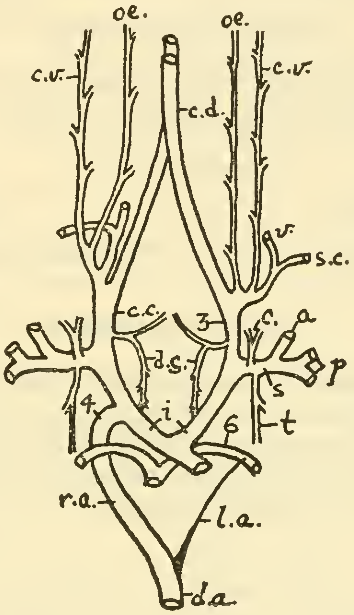

FIGURE 116.—Main cervical and thoracic arteries in *Jacana spinosa*, ventral view. (For explanation of symbols see p. 551.)

SPECIES STUDIED

By Glenny

Actophilornis africana (Gmelin)
Hydrophasianus chirurgus (Scopoli)
Jacana spinosa gymnostoma (Wagler) (2)
Jacana spinosa intermedia (Sclater)

By Garrod

Parra africana=*Actophilornis africana* (Gmelin)

Family ROSTRATULIDAE

Ligamentum botalli is reduced to a linea botalli or completely lacking and vertebrals and superficial cervicals arise separately in *Rostratula benghalensis*.

Ligamentum botalli greatly reduced, ligamentum aortae broad, and vertebrals and superficial cervicals have a short common root from the common carotid in *Nycticryphes semicollaris*.

Species studied

By Glenny

Rostratula benghalensis (Linné) (2)
Nycticryphes semi-collaris (Vieillot) (2)

Family Haematopodidae

Ligamentum botalli very small; vertebrals and superficial cervicals have a common root from the common carotid.

Species studied

By Garrod

Haematopus niger = *Haematopus ostralegus bachmani* Audubon

By Glenny

Haematopus ostralegus malacophaga Salomonsen

Family Charadriidae

Ligamentum botalli seldom present; vertebrals and superficial cervicals have a common root from the common carotid; accessory oesophageal artery arises either as a branch of the left common carotid or from the ventral superficial cervical artery. There is considerable variation in the number and arrangement of the superficial cervical arteries.

Species studied

By Garrod

Vanellus cristatus = *Vanellus vanellus* (Linné)
Charadrius pluvialis = *Pluvialis apricaria* (Linné)
Charadrius hiaticula Linné

By Glenny

Belonopterus chilensis lampronotus (Wagler)
Stephanibyx coronatus (Boddaert)
Hoplopterus spinosus (Linné)
Hoplopterus duvaucelii (Lesson)
Zonifer tricolor (Vieillot)
Squatarola squatarola (Linné)
Pluvialis dominica fulva (Gmelin)
Charadrius hiaticula semipalmatus Bonaparte
Charadrius melodus Ord
Charadrius alexandrinus hesperius Bates
Charadrius alexandrinus nivosus (Cassin)
Charadrius alexandrinus tenuirostris (Lawrence)
Charadrius sanctae-helenae (Harting)
Charadrius vociferus vociferus Linné
Charadrius vociferus ternominatus Bangs and Kennard
Charadrius wilsonia beldingi (Ridgway)
Charadrius wilsonia cinnamominus (Ridgway)
Oreopholus ruficollis (Wagler)

Family SCOLOPACIDAE

Thoracic and cervical arterial arrangement is similar to that of the Charadriidae.

SPECIES STUDIED

By Garrod

Numenius phaeopus (Linné)
Numenius arquata (Linné)
Limosa lapponica (Linné)
Cambetta flavipes=*Tringa flavipes* (Gmelin)
Totanus solitarius=*Tringa solitaria* Wilson
Strepsilas interpres=*Arenaria interpres* (Linné)
Gallinago scolopacina=*Capella gallinago* (Linné)
Gallinago gallinula=*Lymnocryptes minima* (Brünnick)
Scolopax rusticola Linné
Totanus calidris=? *Tringa totanus* (Linné)
Tringa canutus=*Calidris canutus* (Linné)
Machetes pugnax=*Philomachus pugnax* (Linné)
Tringa cinctus=*Eriola alpina* (Linné)

By Glenny

Bartramia longicauda (Bechstein)
Numenius borealis (J. R. Forster)
Numenius tahitiensis (Gmelin)
Numenius arquata (Linné)
Numenius americanus Bechstein
Limosa haemastica (Linné)
Limosa lapponica baueri Naumann
Tringa flavipes (Gmelin)
Tringa melanoleuca (Gmelin)
Tringa solitaria cinnamomea (Brewster)
Tringa solitaria solitaria Wilson
Tringa glareola Linné
Actitis hypoleucos (Linné)
Actitis macularia (Linné) (2)
Catoptrophorus semipalmatus (Gmelin)
Heteroscelus brevipes (Vieillot)
Heteroscelus incanus (Gmelin)
Arenaria interpres (Linné)
Arenaria interpres morinella (Linné)
Arenaria melanocephala (Vigors)
Limnodromus griseus (Gmelin)
Capella stenura (Bonaparte)
Capella delicata (Ord)
Philohela minor (Gmelin)
Calidris canutus rufus (Wilson)
Crocethia alba (Pallas)
Erueunetes pusillus (Linné)
Erueunetes mauri Cabanis
Erolia subminuta (Middendorff)
Erolia minutilla (Vieillot)
Erolia fuscicollis (Vieillot)
Erolia bairdii (Coues)
Erolia melanotos (Vieillot)
Erolia maritima (Brünnich)
Erolia ptilocnemis (Coues)
Erolia alpina sakhalina (Vieillot)
Micropalama himantopus (Bonaparte)
Tryngites subruficollis (Vieillot)
Philomachus pugnax (Linné)

Family RECURVIROSTRIDAE

Ligamentum botalli usually reduced or absent; ductus shawi, vertebral and superficial cervical arteries arise from a common root or branch from the common carotid.

SPECIES STUDIED

By Glenny

Himantopus himantopus himantopus (Linné)
Himantopus himantopus mexicanus (P. L. S. Müller)
Himantopus himantopus melanurus Vieillot
Recurvirostra americana Gmelin

Family Phalaropodidae

Ligamentum botalli absent; vertebrals and superficial cervicals arise separately from the common carotid; type 2 thoracic artery in *Phalaropus fulicarius.*

Species studied

By Glenny

Phalaropus fulicarius (Linné)
Steganopus tricolor Vieillot
Lobipes lobatus (Linné)

Family Dromadidae

Ligamentum botalli reduced to a linea botalli or lacking; vertebrals and superficial cervicals arise separately from the common carotid arteries.

Species studied

By Glenny

Dromas ardeola Paykull

Family Burhinidae

Carotids A–1; no additional information available.

Species studied

By Garrod

Oedicnemus bistriatus=*Burhinus bistriatus* (Wagler)
Oedicnemus grallarius=*Burhinus magnirostris* (Latham)

Family Glareolidae

Ligamentum botalli absent; vertebrals and superficial cervicals have a common root from the common carotid; the accessory oesophageal artery arises as a branch of the left common carotid artery.

Species studied

By Glenny

Cursorius sp.
Glareola maldivarum J. R. Forster (2)

By Garrod

Glareola sp.

Family Thinocoridae

Ligamentum botalli absent; vertebrals and superficial cervicals may or may not have a common root from the common carotid artery; an accessory oesophageal artery arises from the base of the superficial cervical (left side) in *Thinocorus* but was not observed in *Attagis.*

Species studied

By Glenny

Attagis malouinus malouinus (Boddaert)
Thinocorus rumicivorus rumicivorus Eschscholtz (2)

Family Chionididae

Ligamentum botalli prominent; vertebrals and superficial cervicals separate in origin from the common carotid artery; left common carotid gives off an accessory oesophageal artery.

Species studied

By Glenny

Chionis minor minor Hartlaub (2)

Family Stercorariidae

Carotids A–1; no additional information available.

Species studied

By Garrod

Lestris antarcticus = *Catharacta skua antarctica* (Lesson)

Family Laridae

Ligamentum botalli usually absent, but may be present at least in part; vertebrals and superficial cervicals usually have a common root, but this is variable; the left common carotid usually sends off an accessory oesophageal artery. The number and origin of the cervical arteries vary somewhat within the family.

Species studied

By Garrod

Larus argentatus Pontoppidan
Larus glaucus = *Larus hyperboreus* Gunnerus
Sterna hirundo Linné

By Glenny

Larus heermanni Cassin
Larus argentatus Pontoppidan
Larus hyperboreus Gunnerus
Larus philadelphia (Ord)
Rissa tridactyla tridactyla (Linné)
Rissa tridactyla pollicaris Ridgway
Xema sabini (J. Sabine)
Sterna hirundo Linné
Sterna paradisaea Pontoppidan
Sterna vittata Gmelin
Sterna forsteri Nuttall
Sterna albifrons antillarum (Lesson)
Thalasseus bergii (Lichtenstein)
Anoüs stolidus pileatus (Scopoli)
Anoüs minutus melanogenys G. R. Gray
Gygis alba candida (Gmelin)

Family Rynchopidae

Ligamentum botalli greatly reduced or lacking; vertebrals and superficial cervicals have a common root from the common carotid; the left common carotid sends off an accessory oesophageal artery.

Species studied

By Glenny

Rynchops nigra nigra Linné (2)

Family Alcidae

Ligamentum botalli may be present, but more frequently is absent or reduced; vertebrals and superficial cervicals usually have a common root, but this is somewhat variable; the left common carotid generally sends off an accessory oesophageal artery.

Except for two species (noted below), the alcids are bicarotid (A–1).

Species studied

By Garrod

Arctica alle=*Plautus alle* (Linné) (B–4–s)
Alca torda Linné
Uria troile=*Uria aalge aalge* (Pontoppidan)

By Glenny

Alca torda Linné
Uria lomvia arra (Pallas)
Uria aalge inornata Salomonsen
Cepphus grylle (Linné)
Cepphus columba Pallas
Synthliboramphus antiquus (Gmelin) (2) (A–1)
Synthliboramphus antiquus (Gmelin) (5) (B–4–s)
Synthliboramphus wumizusume (Temminck) (2) (A–1)
Cyclorrhynchus psittacula (Pallas) (3)
Aethia cristatella (Pallas)
Aethia pusilla (Pallas)
Aethia pygmaea (Gmelin)
Lunda cirrhata (Pallas)

Order COLUMBIFORMES

Carotids A–1; type 1 thoracic artery; type A and type D coracoid artery—one, two, or rarely three pairs of coracoid arteries may be present; ligamentum aortae present, but may be reduced in size (not observed in a single specimen of *Syrrhaptes paradoxus*); ligamentum botalli usually absent, but when present it may be reduced to a thin ligament, ligamentous button, or a linea botalli; there is considerable variation in the arrangement of the vertebral and superficial cervical arteries—there being no uniformity in the members of this order or within a single species, insofar as the present study can ascertain; an accessory oesophageal artery arises as a branch of the left common carotid or one of the superficial cervical arteries and primarily supplies the crop. There is considerable variation in the cervical arteries in the Columbidae.

References: Beddard, 1898; Bhaduri, 1939; Bhaduri and Biswas, 1954; Gadow, 1891; Garrod, 1873; Glenny, 1940b, 1941a; Glenny and Amadon, 1955; Mathew, 1944; Subhapradha, 1944.

Family Pteroclidae

Ligamentum botalli absent; type A coracoid artery in *Pterocles* sp. and type D coracoid artery observed in *Syrrhaptes paradoxus*.

Species studied

By Garrod

Pterocles arenarius=*Pterocles orientalis* (Linné)
Pterocles alchata (Linné)

By Glenny

Syrrhaptes paradoxus (Pallas)
Pterocles sp.

Family RAPHIDAE

Extinct; no information available.

Family COLUMBIDAE

Ligamentum botalli usually absent; ductus caroticus (right side) frequently persistent; three pairs of coracoid arteries are found in *Otidiphaps nobilis*, normally one or two pairs may be found.

SPECIES STUDIED

By Bhaduri

Columba livia intermedia Strickland

By Bhaduri and Biswas

Columba livia Gmelin
Streptopelia tranquebarica tranquebarica (Herman)
Streptopelia chinensis suratenis (Gmelin)
Streptopelia senegalensis cambayensis (Gmelin)
Chalcophaps indica indica (Linné)
Treron bicincta bicincta (Jerdon)
Treron phoenicoptera phoenicoptera (Latham)

By Garrod

Treron calva (Temminck)
Ptilonopus mariae=*Ptilinopus perousii mariae* (Jacquinot and Pucheran)
Ptilonopus melanocephalus=*Ptilinopus melanospila melanauchen* (Salvadori)
Carpophaga globicera=*Ducula myristicivora* (Scopoli)
Carpophaga aenea=*Ducula aenea* (Linné)
Tympanistria bicolor=*Tympanistria tympanistria* (Temminck)
Lopholaemus antarcticus=*Lopholaimus antarcticus* (Shaw)
Columba livia Gmelin
Columba oenas Linné
Columba leucocephala Linné
Columba picazuro Temminck
Columba maculosa Temminck
Turtur aldabranus=*Streptopelia picturata aldabrana* (Sclater)
Columba vinacea=*Streptopelia vinacea* (Gmelin)
Turtur senegalensis=*Streptopelia senegalensis* (Linné)
Geopelia humeralis (Temminck)
Geopelia striata (Linné)
Geopelia placida=*Geopelia striata placida* Gould
Geopelia cuneata (Latham)
Metriopelia melanoptera (Molina)
Chamaepelia talpacoti=*Columbigallina talpacoti* (Temminck)
Chalcopelia chalcospilos=*Turtur chalcospilos* (Wagler)
Chalcopelia puella=*Turtur brehmeri infelix* Peters
Chalcophaps indica chrysochlora (Wagler)
Phaps chalcoptera (Latham)
Ocyphaps lophotes (Temminck)
Leptoptila jamaicansis (Linné)
Phlogoenas cruentata=*Gallicolumba luzonica* (Scopoli)
Caloenas nicobarica (Linné)
Goüra coronata=*Goüra cristata* (Pallas)
Goüra victoria (Fraser)
Didunculus strigirostris (Jardine)

By Glenny

Sphenurus oxyura (Temminck)
Treron curvirostra (Gmelin)
Phapitreron leucotis nigrorum (Sharpe)
Ptilinopus perousii Peale
Alectroenas pulcherrima (Scopoli)
Megaloprepia magnifica (Temminck)
Ducula pacifica (Gmelin)
Columba livia Gmelin
Columba fasciata Say
Macropygia ruficeps (Temminck)
Ectopistes migratoria (Linné) (2)
Zenaidura macroura carolinensis (Linné) (2)
Zenaida asiatica mearnsi (Ridgway)
Nesopelia galapagoensis (Gould)
Streptopelia sp.
Streptopelia orientalis (Latham)
Streptopelia chinensis (Scopoli)
Geopelia striata (Linné)
Columbina picui (Temminck)
Columbigallina passerina insularis Ridgway

Oena capensis (Linné)
Turtur sp.
Chalcophaps indica (Linné)
Ocyphaps lophotes (Temminck)
Geophaps smithii (Jardine and Selby)
Leptotila verreauxii (Bonaparte)
Oreopeleia caniceps leucometopius Chapman
Gallicolumba xanthonura (Temminck)
Otidiphaps nobilis Gould (2)
Caloenas nicobarica (Linné)
Goüra cristata (Pallas)
Didunculus strigirostris (Jardine)

Order PSITTACIFORMES

Carotids A–1, A–2–s, B–2–s, B–3b–d to B–4–s; type A coracoid artery; type 1 thoracic artery; ligamentum aortae present; ligamentum botalli usually absent, or when present much reduced or remains as a linea botalli; vertebrals and superficial cervicals have a common root from the common carotid artery, with but a few individual exceptions; an accessory oesophageal artery from the left carotid may be present, but not necessarily so in all of the species.

References: Beddard, 1898; Bhaduri and Biswas, 1945; Garrod, 1873; Glenny, 1940a, 1951c; Mackay, 1887; Meckel, 1826.

Family Psittacidae

Subfamily Strigopinae

Carotids A–1; no additional information available.

Species studied

By Garrod

Strigops habroptilus G. R. Gray

Subfamily Nestorinae

Carotids A–2–s; accessory oesophageal artery from the left common carotid artery.

Species studied

By Garrod

Nestor notabilis Gould
Nestor hypopolius = *Nestor meridionalis* (Gmelin)

By Glenny

Nestor meridionalis (Gmelin)

Subfamily Loriinae

Carotids A–1, except in *Lathamus discolor* (A–2–s). A notable ductus caroticus was observed in a specimen of *Trichoglossus haematod forsteni* (USNM 319456) (fig. 117).

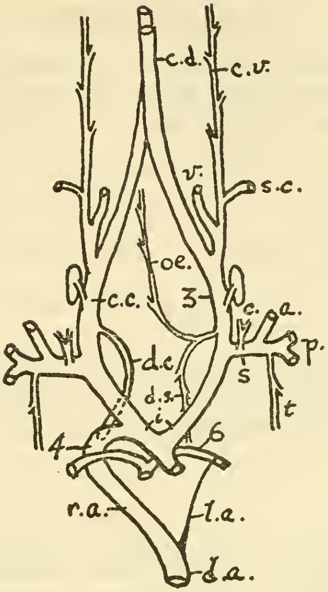

Figure 117.—Main cervical and thoracic arteries in *Trichoglossus haematod forsteni*, ventral view. (For explanation of symbols see p. 551.)

Species studied

By Garrod

Lorius cardinalis = *Chalcopsitta cardinalis* (G. R. Gray)
Eos indica = *Eos histrio* (P. L. S. Müller)
Trichoglossus concinnus = *Glossopsitta concinna* (Shaw)
Lathamus discolor (White) (A–2–s)

By Glenny

Chalcopsitta sintillata (Temminck)
Eos cyanogenia Bonaparte
Eos squamata guenbyensis (Scopoli)
Eos bornea (Linné)
Trichoglossus ornatus (Linné)
Trichoglossus haematod moluccanus (Gmelin)
Trichoglossus haematod forsteni Bonaparte
Trichoglossus chlorolepidotus (Kuhl)
Pseudeos fuscata (Blyth)
Domicella hypoinochroa devittata (Hartert)
Domicella lory (Linné)
Domicella chlorocercus (Gould)
Domicella garrula (Linné)
Phigys solitarius (Suckow)
Vini australis (Gmelin) (2)
Vini kuhlii (Vigors)
Vini stepheni (North)
Vini peruviana (P. L. S. Müller)
Glossopsitta concinna (Shaw)
Glossopsitta porphyrocephala (Dietrichsen)
Charmosyna placentis subplacens (Sclater) (2)
Charmosyna pulchella G. R. Gray
Opopsitta sp.
Lathamus discolor (White) (A–2–s)

Subfamily Micropsittinae

Carotids A–1; ligamentum aortae greatly reduced; ligamentum botalli absent; vertebrals and superficial cervicals have a common root from the common carotid artery.

Species studied

By Glenny

Micropsitta pusio pusilla (Ramsay)

Micropsitta finschii (Ramsay)

Subfamily Kakatoeinae

Carotids A–1 and unicarotid (see list of species below); ligamentum botalli present in *Calyptorhynchus magnificus* and *Kakatoe galerita;* ligamentum aortae almost completely absent in *Nymphicus hollandicus.*

Species studied

By Garrod

Cacatua galerita=*Kakatoe galerita* (Latham) (laevo-carotid)

Cacatua cristata=*Kakatoe sulphurea citrino-cristata* (Fraser) (laevo-carotid)

Eolophus roseicapillus=*Kakatoe roseicapilla* (Vieillot) (bicarotid: A–1)

Calopsitta novae-hollandiae=*Nymphicus hollandicus* (Kerr) (bicarotid)

By Glenny

Calyptorhynchus magnificus (Shaw) (A–1)

Callocephalon fimbriatum (Grant) (A–1)

Kakatoe galerita (Latham) (2) (B–3b–d)

Kakatoe leadbeateri (Vigors) (B–3b–d)

Kakatoe sanguinea (Gould) (B–3b–d)

Nymphicus hollandicus (Kerr) (A–1)

By Mackay

Cacatua sulphurea=*Kakatoe sulphurea* (Gmelin) (B–2–s)

By Meckel

Kakatoe sulphurea (Gmelin) (B–2–d)

It is my opinion that the Meckel report is more accurate, although the Mackay report could be true. It is possible that a typographical error may have been made in the reporting of Mackay's work. The B–2–d arrangement is to be expected in the *Kakatoe* series.

Subfamily Psittacinae

Carotids A–1 and A–2–s. All South American parrots have the A–2–s arrangement.

Species studied

By Bhaduri and Biswas

Psittacula krameri manillensis (Bechstein) (A–1)

Psittacula cyanocephala cyanocephala (Linné) (A–1)

By Garrod

(Species with A–2–s carotid)

Ara macao (Linné)

Conurus holochlorus=*Aratinga holochlora* (Sclater)

Conurus jandaya=*Aratinga jandaya* (Gmelin)

Conurus petzi=*Aratinga canicularis* (Linné)

Conurus cruentatus=*Pyrrhura crueniata* (Wied)

Psittacula passerina=*Forpus passerinus flavissimus* Hellmayr
Brotogerys tiriacula=*Brotogeris tirica* (Gmelin)
Brotogerys virescens=*Brotogeris versicolurus* (P. L. S. Müller)
Brotogerys tui=*Brotogeris chrysopterus tuipara* (Gmelin)
Caïca melanocephala=*Pionites melanocephala* (Linné)
Pionus menstruus (Linné)
Chrysotis festiva=*Amazona festiva* (Linné)
Chrysotis levaillantii=*Amazona ochrocephala oratrix* Ridgway
Chrysotis ochrocephala=*Amazona ochrocephala* (Gmelin)
Conurus xantholaemus=*Aratinga pertinax* (Linné)
Psittacus erithacus Linné
Platycercus eximius (Shaw)
Platycercus pallidiceps=*Platycercus adsciyus palliceps* Lear
Psephotus haematogaster=*Northiella haematogaster* (Gould)
Cyanoramphus novaezelandiae (Sparrmann)
Cyanoramphus auriceps (Kuhl)

(Species with A–1 carotid)

Prioniturus sp.
Palaeornis alexandri=*Psittacula alexandri* (Linné)
Aprosmictus scapulatus=*Alisterus scapularis* (Lichtenstein)
Agapornis roseicollis (Vieillot)
Loriculus sp.
Euphema pulchella=*Neophema pulchella* (Shaw)
Euphema splendida=*Neophema splendida* (Gould)
Euphema bourkii=*Neophema bourkii* (Gould)
Melopsittacus undulatus (Shaw)

By Glenny

(Species with A–2–s carotid)

Ara ararauna (Linné)
Ara auricollis Cassin
Aratinga guarouba (Gmelin)
Aratinga holochlora (Sclater)
Aratinga auricapillus (Kuhl)
Aratinga nana (Vigors)
Aratinga canicularis (Linné)
Aratinga pertinax (Linné) (2)
Aratinga aurea (Gmelin)
Nandayus nenday (Vieillot)
Conuropsis carolinensis carolinensis (Linné)
Rhynchopsitta pachyrhyncha (Swainson)
Cyanoliseus patagonus (Vieillot)
Microsittace ferruginea (P. L. S. Müller) (2)
Myiopsitta monachus colorra (Vieillot)
Bolborhynchus lineola (Cassin)
Forpus passerinus viridissimus (Lafresnaye) (2)
Forpus sclateri eidos Peters
Forpus coelestis (Lesson)
Brotogeris tirica (Gmelin)
Brotogeris versicolurus versicolurus (P. L. S. Müller)
Brotogeris versicolurus chiriri (Vieillot)
Brotogeris jugularis (P. L. S. Müller) (3)
Brotogeris cyanoptera (Pelzeln)
Pionites melanocephala (Linné)
Pionopsitta pileata (Scopoli)
Graydidascalus brachyurus (Kuhl)
Pionus menstruus (Linné) (2)
Amazona ventralis (P. L. S. Müller)
Amazona agilis (Linné)
Amazona barbadensis rothschildi (Hartert)
Amazona ochrocephala oratrix Ridgway
Amazona ochrocephala ochrocephala (Gmelin)
Amazona amazonica amazonica (Linné)
Deroptyus accipitrinus (Linné)
Poicephalus senegalus (Linné)
Poicephalus meyeri (Cretzschmar)
Psittacus erithacus Linné (2)
Coracopsis vasa drouhardi Lavauden
Psittrichas fulgidus (Lesson)
Prosopeia tabuensis tabuensis (Gmelin)
Prosopeia tabuensis splendens (Peale)
Psephotus chrysopterygius Gould
Platycercus elegans (Gmelin)
Platycercus caledonicus flaveolus Gould
Platycercus eximius (Shaw)
Platycercus zonarius barnardi Vigors and Horsfield
Northiella haematogaster haematorrhous (Gould)
Cyanoramphus novaezelandiae (Sparrman)
Cyanoramphus auriceps (Kuhl)

(Species with A–1 carotid)

Lorius roratus (P. L. S. Müller)
Tanygnathus lucionensis (Linné)
Psittacula longicauda longicauda (Boddaert)
Psittacula longicauda tytleri (Hume)
Polytelis anthopeplus (Lear)
Alisterus scapularis (Lichtenstein)
Agapornis cana (Gmelin)
Agapornis cana ablectanea Bangs
Agapornis taranta (Stanley)
Agapornis fischeri Reichenow
Agapornis personata Reichenow
Agapornis lilianae Shelley
Loriculus beryllinus (J. R. Forster)
Loriculus galgulus (Linné) (2)
Melopsittacus undulatus (Shaw) (2)

Order CUCULIFORMES

Carotids chiefly A–1, but A–3, A–4, and A–3–s/A–4–d also observed; type A coracoid artery; type 1 thoracic artery; ligamentum aortae present, but may be reduced; ligamentum botalli usually lacking, or much reduced when present; vertebrals and superficial cervicals vary in origin from the common carotid arteries.

References: Bhaduri and Biswas, 1945; Garrod, 1873; Glenny, 1941b.

Family MUSOPHAGIDAE

Vertebrals and superficial cervicals have separate points of origin from the common carotid arteries; an accessory oesophageal artery arises as a branch from the left common carotid artery or from the left superficial cervical artery.

Both the ligamentum aortae and the ligamentum botalli are prominent in *Tauraco leucotis donaldsoni*, whereas in *Tauraco macrorhynchus verreauxii* and *Crinifer leucogaster* the ligamentum aortae is much reduced and the ligamentum botalli is absent.

SPECIES STUDIED

By Garrod

Musophaga violacea Isert
Corythaix albocristata = *Tauraco corythaix* (Wagler)
Schizorhis africana = *Crinifer africanus* (Latham)

By Glenny

Tauraco leucotis donaldsoni (Sharpe)
Tauraco macrorhynchus verreauxii (Schlegel)
Crinifer leucogaster (Rüppell)

Family CUCULIDAE

Carotids A–1, with but a few exceptions (see list of species below).

Bhaduri and Biswas (1945) reported that both left and right ascending oesophageal arteries arise in common with the superficial cervical (comes nervi vagi) arteries as a branch of the vertebrals in *Eudynamys scolopaceas*, and the ascending oesophageal is shown to connect anteriorly with the cephalic external carotids. This is further evidence that the ascending oesophageal arteries are functionally modified ventral carotids and is in accord with Hughes' (1934) observations in the chick embryo.

In *Zanclostomus javanicus* and *Phaenicophaeus pyrrhocephalus* both dorsal carotids are superficial and do not enter the hypapophysial canal (infranormales), but lie on either side of the oesophagus to which organ they supply blood (A–3). Meckel (1826) suggested that this arrangement of the carotids might be expected in some species of bird.

A still further modification in the arrangement of the dorsal carotids is found in a specimen of *Rhamphococcyx curvirostris erythrognathus* (USNM 223471). In this specimen the left dorsal carotid serves as a much-reduced ascending oesophageal artery, while the right dorsal carotid is reduced to a small ligament which enters the hypapophysial canal (A–3–s/A–4–d); the right superficial cervical artery sends off branches to the oesophagus.

Yet another modification of the bicarotid arrangement is found in *Rhopodytes viridirostris*. In this species, both dorsal carotids are reduced to ligamenti ottleyi which enter the hypapophysial canal (A–4).

In each of the above mentioned species, the vertebrals and superficial cervicals were notably enlarged and appeared to carry an increased amount of blood to the head region.

SPECIES STUDIED

By Bhaduri and Biswas

Eudynamis s. scolopaceus = *Eudynamys s. scolopacea* (Linné)

By Garrod

Cuculus canorus Linné
Cacomantis variolosus sepulcralis (S. Müller)
Chrysococcyx sp.
Phaenicophaes sp. = *Phaenicophaeus pyrrhocephalus* (Pennant)
Guira piririgua = *Guira guira* (Gmelin)
Centropus senegalensis (Linné)

By Glenny

Cuculus sp.
Cacomantis pyrrophanus schistaceigularis Sharpe
Chrysococcyx cupreus intermedius Hartlaub
Chalcites lucidus layardi (Mathews)
Surniculus lugubris (Horsfield)
Urodynamis taitensis (Sparrmann)
Coccyzus erythrophthalamus (Wilson)
Coccyzus cinereus Vieillot
Coccyzus americanus (Linné) (2)
Piaya rufigularis (Hartlaub)
Saurothera merlini d'Orbigny (2)
Ceuthmochares aereus (Vieillot)
Rhopodytes viridirostris (Jerdon) (A–4)
Rhinortha chlorophaea (Raffles)
Zanclostomus javanicus (Horsfield) (A–3)
Rhamphococcyx curvirostris erythrognathus (Bonaparte) (A–3–s/A–4–d)
Phaenicophaeus pyrrhocephalus (Pennant) (A–3)
Crotophaga ani Linné (3)
Guira guira (Gmelin) (2)
Tapera naevia chochi (Vieillot)
Geococcyx californiana (Lesson)
Neomorphus geoffroyi salvini Sclater
Coua caerulea (Linné)
Centropus bengalensis javanensis (Dumont)

Order STRIGIFORMES

Carotids A-1; type C coracoid artery usually, but type A occurs more rarely; type 1 thoracic artery; ligamentum aortae usually prominent; ligamentum botalli present, but may be greatly reduced; vertebrals and superficial cervicals arise separately from the common carotid; an accessory oesophageal artery arises as a branch of the left common carotid artery.

References: Garrod, 1873; Glenny, 1943c.

Family Tytonidae

Species studied

By Glenny

Tyto alba (Scopoli) (2)

Family Strigidae

Species studied

By Garrod

Bubo fasciolatus=*Bubo poensis* Fraser
Scops zorca=*Otus scops* (Linné)
Otus vulgaris=*Asio otus* (Linné)
Bubo maximus=*Bubo bubo* (Linné)
Bubo virginianus (Gmelin)
Bubo bubo bengalensis (Franklin)
Bubo capensis A. Smith
Bubo poensis Fraser
Ketupa javanensis=*Ketupa ketupa* (Horsfield)
Pulsatrix torquata=*Pulsatrix perspicillata* (Latham)
Surnia funerea=*Surnia ulula* (Linné)
Glaucidium sp.
Athene passerina=*Glaucidium passerinum* (Linné)
Athene noctua (Scopoli)
Athene brama (Temminck)
Phaleoptynx cunicularia=*Speotyto cunicularia* (Molina)
Syrnium aluco=*Strix aluco* Linné
Syrnium nebulosum=*Strix nebulosa* J. R. Forster
Strix flammea=*Asio flammeus* (Pontoppidan)

By Glenny

Otus asio (Linné) (3)
Bubo virginianus (Gmelin) (2)
Nyctea scandiaca (Linné) (4)
Strix varia Barton (2)
Rhinoptynx clamator (Vieillot)
Asio otus wilsonianus (Lesson) (2)
Asio flammeus (Pontoppidan)
Aegolius acadicus (Gmelin) (2)

Order CAPRIMULGIFORMES

Both bicarotid and unicarotid arrangements are found; coracoid artery types A, B, C, and D occur; type 1 thoracic artery; ligamentum aortae present; presence of the ligamentum botalli variable; origin of the vertebrals and superficial cervicals variable.

References: Garrod, 1873; Glenny, 1953c.

Family Steatornithidae

Carotids A–1; type A coracoid; ligamentum botalli present; vertebrals and superficial cervicals have a short common root from the common carotid artery.

Species studied

By Garrod	By Glenny
Steatornis caripensis Humboldt	*Steatornis caripensis* Humboldt

Family Podargidae

Unicarotid (see list of species below); coracoid artery types B, C, and D (see list of species below); ligamentum botalli absent, or present as a linea botalli; vertebrals and superficial cervicals arise separately, for the most part, from the common carotid; an ascending oesophageal artery arises from the right common carotid artery.

In a single specimen of *Podargus papuensis* a patent ductus caroticus was observed. This group appears to be undergoing further evolution of the aortic arch system.

Species studied

By Glenny

Podargus strigoides (Latham) (B–4–s) (B)
Podargus papuensis Quoy and Gaimard (B–4–s) (D)
Podargus ocellatus Quoy and Gaimard (B–2–d) (A/B)
Batrachostomus hodgsoni indochinae Stresemann (B–4–s) (C)

Family Nyctibiidae

Carotids B–4–s; type C coracoid artery; ligamentum botalli absent; vertebrals and superficial cervicals arise from the common carotid artery at about the same site, or may have a short common root from the common carotid.

Species studied

By Glenny

Nyctibius griseus (Gmelin)

Family Aegothelidae

Carotids A–1; type D coracoid artery; ligamentum botalli absent; vertebrals and superficial cervicals arise separately from the common carotid arteries.

Species studied

By Glenny

Aegotheles sp. (Lake Habbema, New Guinea)

Family Caprimulgidae

Carotids A–1; coracoid artery types A, B, and C occur (see list of species below); ligamentum botalli may be complete, reduced, or absent; vertebrals and superficial cervicals arise separately from the common carotids.

Species studied

By Garrod

Chordeiles acutipennis texensis Lawrence
Caprimulgus europaeus Linné

By Glenny

Lurocalis semitorquatus (Gmelin) (A)
Chordeiles minor minor (J. R. Forster) (B)
Chordeiles minor vicinus Riley (B, C)
Nyctiprogne leucopyga (Spix) (C)
Podager nacunda (Vieillot) (2) (A)
Nyctidromus albicollis (Gmelin) (A)
Caprimulgus carolinensis Gmelin (C)
Caprimulgus longirostris Bonaparte (B)
Scotornis fossii (Hartlaub) (A)
Semeïophorus vexillarius Gould (A)
Hydropsalis brasiliana furcifera (Vieillot) (A)

Order APODIFORMES

Both bicarotid and unicarotid arrangements occur, but the unicarotid arrangement is of more frequent occurrence; coracoid artery types A and E occur; type 1 thoracic artery; ligamentum aortae present; ligamentum botalli usually absent but may be found in a few individuals; vertebrals and superficial cervicals generally have separate points of origin from the common carotids, but usually are very close together.

References: Garrod, 1873; Glenny, 1953b.

Family Apodidae

Both bicarotid and unicarotid arrangements (see list of species below); type A coracoid artery; ligamentum botalli absent.

Species studied

By Garrod

Chetura caudacuta=*Hirund-apus caudacutus* (Latham) (B–4–s)
Chetura vauxi=*Chaetura vauxi* (J. K. Townsend) (B–4–s)
Chetura spinicauda=*Chaetura spinicauda* (Temminck) (B–4–s)
Cypseloides fumigatus (Streubel) (A–1)
Cypselus alpinus=*Apus melba* (Linné) (B–4–s)
Cypselus apus=*Apus apus* (Linné) (B–4–s)

By Glenny

Collocalia inexpectata bartschi Mearns (B–4–s)
Streptoprocne zonaris pallidifrons (Hartert) (A–1)
Streptoprocne zonaris albicincta (Cabanis) (2) (A–1)
Chaetura vauxi (J. K. Townsend) (B–3b–d)
Chaetura pelagica (Linné) (3) (B–4–s)
Chaetura cinereiventris guianensis Hartert (2) (B–3b–d)
Nephoecetes niger (Gmelin) (A–1)
Apus andecolus (d'Orbigny and Lafresnaye) (B–4–s)
Aëronautes saxatalis (Woodhouse) (3) (B–4–s)
Tachornis phoenicobia Gosse (B–3b–d)

Family HEMIPROCNIDAE

Carotids B–4–s; type A coracoid artery; ligamentum botalli may be present, but much reduced.

SPECIES STUDIED

By Garrod	By Glenny
Dendrochelidon coronata=*Hemiprocne longipennis* (*coronata*) (Tickell) (B–4–s)	*Hemiprocne comata major* (Hartert)
	Hemiprocne mystacea aëroplanes Stresemann

Family TROCHILIDAE

Carotids B–4–s; coracoid artery types A and E (see list of species below); ligamentum botalli absent. The functional equivalent of the systemic arch usually arises as a branch of the right innominate artery just posterior to the point of origin of the subclavian and common carotid arteries (fig. 118).

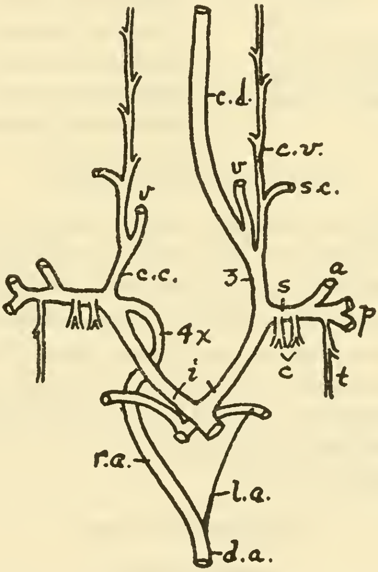

FIGURE 118.—Main cervical and thoracic arteries in the Trochilidae, ventral view. (For explanation of symbols see p. 551.)

The right ductus caroticus comes to serve as the functional systemic arch (Glenny, 1953c, 1954c).

Species studied

By Garrod

Chlorolampis osberti=*Chlorostilbon canivetii osberti* Gould
Patagona gigas (Vieillot)

By Glenny

Glaucis hirsuta (Gmelin) (E)
Phaethornis sp. (E)
Campylopterus falcatus (Swainson) (E)
Florisuga mellivora (Linné) (E)
Anthracothorax dominicus (Linné) (E)
Eulampis jugularis (Linné) (E)
Sericotes holosericeus (Linné) (E)
Chrysolampis mosquitus (Linné) (E)
Orthorhynchus cristatus exilis (Gmelin) (E)
Klais guimeti (Bourcier) (E)
Lophornis sp. (E)
Chlorostilbon canivetii caribaeus Lawrence (E)
Chlorostilbon ricordii (Gervais) (E)
Cynanthus latirostris Swainson (E)
Thalurania furcata colombica (Bourcier) (A)
Lepidopyga goudoti (Bourcier) (E)
Hylocharis xantusii (Lawrence) (E)
Hylocharis chrysura (Shaw) (E)
Trochilus polytmus Linné (E)
Leucippus fallax (Bourcier) (E)
Amazilia tobaci feliciae (Lesson) (3) (E)
Amazilia tzacatl (de la Llave) (E)
Chalybura buffonii aeneicauda Lawrence (E)
Chalybura buffonii subsp. (A)
Oreotrochilus leucopleurus Gould (E)
Patagona gigas (Vieillot) (E)
Sephanoides fernandensis (King) (E)
Sephanoides sephanoides (Lesson) (E)
Aglaiocercus kingi margarethae (Heine) (2) (E)
Sappho sparganura sapho (Lesson) (E)
Heliomaster furcifer (Shaw) (E)
Philodice evelynae (Bourcier) (E)
Archilochus colubris (Linné) (2) (E)
Mellisuga minima vieilloti (Shaw) (E)
Stellula calliope (Gould) (A)
Selasphorus platycercus (Swainson) (E)

Order COLIIFORMES

Carotids B–4–s; type A coracoid artery; thoracic artery types 3 and 4; ligamentum aortae present; ligamentum botalli greatly reduced and may fuse with the radix aortae and remain as a linea botalli; vertebral and superficial cervical of the left side arise as branches of a common root from the common carotid; an accessory oesophageal artery arises as a branch of the common carotid on the left side, while the complimentary right oesophageal artery arises from the common carotid at the base of the right vertebral artery.

References: Glenny, 1944e.

Family Coliidae

Species studied

By Glenny

Colius striatus Gmelin
Colius indicus Latham
Colius macrourus (Linné)

Order TROGONIFORMES

Carotids B–4–s; type A coracoid artery except for a specimen of *Trogon rufus* (type B); type 1 thoracic artery; ligamentum aortae present; ligamentum botalli greatly reduced (may remain as a ligamentous button or as a linea botalli); left vertebral and superficial cervical arteries have a common origin from the common carotid artery; an accessory oesophageal artery arises as a branch from either the common carotid or left vertebrocervical root.

References: Garrod, 1873; Glenny, 1943a, 1945b.

Family Trogonidae

Species studied

By Garrod

Trogon mexicanus Swainson
Trogon puella=*Trogon collaris puella* Gould

By Glenny

Pharomachrus mocino costaricensis Cabanis
Priotelus temnurus (Temminck)
Temnotrogon roseigaster (Vieillot)
Trogon massena Gould
Trogon melanuras macroura Gould
Trogon strigilatus Linné
Trogon citreolus melanocephala Gould
Trogon collaris exoptatus Cabanis and Heine
Trogon rufus tenellus Cabanis
Trogon rufus Gmelin (B)
Trogon surrucura Vieillot
Trogon curucui behni Gould
Trogon violaceus caligatus Gould
Apaloderma narina (Stephens)
Harpactes erythrocephalus (Gould)

Order CORACIIFORMES

Carotids both bicarotid and unicarotid arrangements occur; type A coracoid artery except in one species thus far noted; thoracic artery varies in the several families; ligamentum aortae present, except in a few instances in which the radix aortae of the left side remains as a functional vessel; presence of the ligamentum botalli is variable; origin of the vertebrals and superficial cervicals varies in the different families.

References: Beddard, 1898; Bhaduri and Biswas, 1945; Garrod, 1873, 1876; Glenny, 1939, 1943b; Ottley, 1879.

Family Alcedinidae

Carotids A-1; thoracic artery usually type 1, but may vary (see list of species below); ligamentum botalli may be present or absent; vertebrals and superficial cervicals usually arise as branches from a common root from the common carotid; an accessory oesophageal may be present and arise as a branch of the left carotid artery.

Species studied

By Garrod

Ceryle maxima (Pallas)
Ceryle amazona=*Chloroceryle amazona* (Latham)
Alcedo atthis ispida Linné
Dacelo gigantea=*Dacelo novaguineae* (Hermann)
Dacelo leachii cervina Gould
Cittura cyanotis (Temminck)
Halcyon sp.

By Glenny

Ceryle torquata (Linné) (2)
Ceryle alcyon (Linné) (7) (Type 2 thoracic)
Ceryle rudis (Linné) (Type 3 thoracic)
Chloroceryle amazona (Latham) (2)
Chloroceryle americana septentrionalis (Sharpe)
Chloroceryle americana isthmica (Goldman)

Alcedo atthis bengalensis Gmelin
Alcedo coerulescens Vieillot
Alcedo cristata Pallas
Dacelo novaeguineae (Hermann)
Halycon senegalensis (Linné) (Type 6 thoracic, type D coracoid)
Halcyon cheliculi (Stanley) (Type 3 thoracic)
Halcyon cinnamomina Swainson (Type 6 thoracic)
Halcyon chloris (Boddaert)

Family Todidae

Carotids A–1 generally (see list of species below); type 1 thoracic artery; ligamentum botalli usually absent; origin of vertebrals and superficial cervicals variable; an accessory oesophageal artery arises as a branch of the left common carotid artery.

Species studied

By Glenny

Todus multicolor Gould
Todus angustirostris Lafresnaye (B–4–s)
Todus mexicanus Lesson
Todus subulatus G. R. Gray

Family Momotidae

Carotids A–1; type 1 and type 2 thoracic artery (see list of species below); ligamentum botalli present—may be much reduced or remain as a linea botalli; vertebrals and superficial cervicals arise separately from the common carotid artery.

Species studied

By Garrod

Eumomota superciliaris=*Eumomota superciliosa* (Sandbach)
Momotus momota lessonii Lesson

By Glenny

Eumomota superciliosa (Sandbach) (Type 1 thoracic)
Baryphthengus ruficapillus martii (Spix) (2) (Type 2 thoracic)
Momotus momota coeruliceps (Gould) (Type 1 thoracic)
Momotus momota conexus Thayer and Bangs (Type 1 thoracic)

Family Meropidae

Carotids A–1 and B–4–s (see list of species below); type 1 thoracic artery; ligamentum botalli usually absent, or may remain as a linea botalli; vertebrals and superficial cervicals usually arise separately from the common carotids, but the points of origin of these vessels are very close to each other; an accessory oesophageal artery is generally present as a branch of the left common carotid artery.

Species studied

By Garrod

Merops apiaster Linné (B–4–s)
Merops ornatus Latham (B–4–s)

By Glenny

Melittophagus pusillus (P. L. S. Müller) (A–1)
Melittophagus variegatus (Vieillot) (A–1)
Aerops albicollis (Vieillot) (B–4–s)
Merops apiaster Linné (B–4–s)
Merops superciliosus Linné (B–4–s)
Merops orientalis Latham (B–4–s)

Families Leptosomatidae and Brachypteraciidae

No information is available.

Family Coraciidae

Carotids A–1; type 1 thoracic artery; presence of the ligamentum botalli is variable; origin of vertebrals and superficial cervicals variable, although these vessels tend to have a common root from the common carotid arteries.

Species studied

By Garrod	By Glenny
Coracias garrulus Linné	*Coracias caudata* Linné
Eurystomus sp.	*Eurystomus orientalis* (Linné)

Family Upupidae

Carotids B–4–s; type 3 thoracic artery; ligamentum botalli reduced to a linea botalli; vertebrals and superficial cervicals have a common root from the common carotids.

Species studied

By Garrod	By Glenny
Upupa epops Linné	*Upupa epops epops* Linné
	Upapa epops africana Bechstein

Family Phoeniculidae

Carotids B–4–s; type 2 thoracic artery; ligamentum botalli reduced to a linea botalli; vertebrals and superficial cervicals arise separately from the common carotids; an accessory oesophageal artery arises as a branch of the left carotid artery.

Species studied

By Glenny

Phoeniculus purpureus erythrorhynchos (Latham)

Family Bucerotidae

Both bicarotid and unicarotid arrangements occur (see list of species below); type 1 thoracic artery; ligamentum botalli usually present, but may be reduced or lacking in some species; there is considerable variation in the cervical arteries, but the vertebrals and superficial cervicals appear to arise separately from the common carotid arteries; the left superficial cervical generally sends off an accessory oesophageal artery.

SPECIES STUDIED

By Beddard

Aceros sp.
Bucorvus sp.

By Fürbringer

Bucorvus abyssinicus (Boddaert)

By Garrod

Toccus melanoleucus = *Tockus alboterminatus australis* (Roberts) (B–4–s)
Buceros plicatus = *Aceros plicatus* (J. R. Forster) (A–1)
Buceros coronatus = *Anthracoceros coronatus* (Boddaert) (A–1)
Buceros atratus = *Certogymna atrata* (Temminck) (A–1)
Buceros rhinoceros Linné (A–1)
Buceros bicornis Linné (A–1)
Bucorvus abyssinicus (Boddaert) (A–4)

By Glenny

Tockus alboterminatus (Büttikofer) (B–3a–d)
Tockus alboterminatus australis (Roberts) (2) (B–3a–d)
Tockus flavirostris (Rüppell) (B–3a–d)
Aceros undulatus (Shaw) (A–1)
Anthracoceros coronatus convexus (Temminck) (A–1)

By Ottley

Bucorvus abyssinicus (Boddaert) (A–4)

Order PICIFORMES

Carotids B–4–s, except in the Galbulidae (A–1); both the coracoid and thoracic arteries are variable in location; ligamentum aortae present but may be much reduced in some species; presence of the ligamentum botalli is variable; vertebrals and superficial cervicals variable in origin from the common carotid arteries.

References: Bhaduri and Biswas, 1945, 1947; Garrod, 1873, Glenny, 1944a.

Family GALBULIDAE

Carotids A–1; both coracoid and thoracic arteries may be variable (see list of species below); ligamentum botalli absent; vertebrals and superficial cervicals variable in origin, but usually arise separately from the common carotid.

SPECIES STUDIED

By Garrod

Galbula albirostris Latham
Urogalba paradisea = *Galbula dea amazonum* (Sclater)

By Glenny

Galbula ruficauda Cuvier (A) (Type 4 thoracic)

Family BUCCONIDAE

Carotids B–4–s; coracoid and thoracic arteries variable (see list of species below); ligamentum botalli reduced to a linea botalli or lacking; origin of vertebrals and superficial cervicals variable; an accessory oesophageal artery arises as a branch of the left common carotid artery.

SPECIES STUDIED

By Glenny

Notharchus macrorhynchos cryptoleucus van Rossem (A) (Type 1 thoracic)

Notharchus macrorhynchos hyperrhynchus (Sclater) (A) (Type 1 thoracic)

Notharchus pectoralis (G. R. Gray) (A) (Type 3 thoracic)

Nystalus maculatus striatipectus (Sclater) (B) (Type 4 thoracic)

Nonnula frontalis (Sclater) (B) (Type 4 thoracic)

Monasa morphoeus (Hahn and Kuster) (A) (Type 4 thoracic)

Family CAPITONIDAE

Carotids B–4–s (one reported instance of B–4–d); coracoid and thoracic arteries variable (see list of species below: type 3 unless otherwise noted); ligamentum botalli reduced, may occur as a linea botalli or be entirely lacking; vertebrals and superficial cervicals usually arise separately from the common carotid, or may have a short common root; accessory oesophageal artery arises as a branch of the common carotid or left superficial cervical artery.

SPECIES STUDIED

By Bhaduri and Biswas

Thereiceryx zeylanicus caniceps=*Megalaima zeylanica caniceps* (Franklin) (B–4–s and B–4–d) (A) (Type 4 thoracic)

Cyanops a. asiatica=*Megalaima a. asiatica* (Latham) (A)

Xantholaema haemacephala lutea=*Megalaima haemacephala indica* (Latham) (B)

By Garrod

Megalaima asiatica (Latham)

Barbatula duchaillui=*Pogoniulus duchaillui* (Cassin)

By Glenny

Semnornis frantzii (Sclater) (A)

Psilopogon pyrolophus S. Müller (B) (Type 4 thoracic)

Megalaima zeylanica (Gmelin) (A)

Megalaima rafflesii borneensis (W. Blasius) (A)

Megalaima asiatica (Latham) (A)

Megalaima rubricapilla (Gmelin) (B)

Megalaima haemacephala rosea (Dumont) (A)

Megalaima haemacephala (P. L. S. Müller) (B)

Tricholaema leucomelan (Boddaert) (A) (Type 4 thoracic)

Tricholaema diadematum (Heuglin) (A) (Type 5 thoracic)

Lybius leucocephalus albicauda (Shelley) (A) (Type 2 thoracic)

Family INDICATORIDAE

Carotids B–4–s; type A coracoid artery; type 1 thoracic artery; ligamentum botalli reduced to a small basal button or completely lacking; vertebrals and superficial cervicals usually arise separately from the common carotids; accessory oesophageal artery arises as a branch of the left carotid artery.

SPECIES STUDIED

By Glenny

Prodotiscus insignis (Cassin)

Indicator minor Stephens

Indicator indicator (Sparrman)

Indicator xanthonotus fulvus D. Ripley

By Garrod

Indicator major=*Indicator indicator* (Sparrman)

Family RAMPHASTIDAE

Carotids B–4–s; type A coracoid artery; thoracic artery varies (see list of species below); ligamentum botalli may be present or absent; vertebrals and superficial cervicals arise separately from the common carotid arteries; accessory oesophageal artery arises as a branch of the left carotid, left superficial cervical, or near the base of the left vertebral artery.

SPECIES STUDIED

By Garrod

Ramphastos ariel=*Ramphastos vitellinus ariel* Vigors

Ramphastos carinatus=?*Ramphastos sulfuratus* Lesson

Ramphastos cuvieri Wagler

By Glenny

Aulacorhynchus sulcatus (Swainson) (2) (Type 4 thoracic)

Pteroglossus torquatus (Gmelin) (Type 3 thoracic)

Pteroglossus torquatus frantzii Cabanis (Type 3 thoracic)

Selenidera spectabilis Cassin (Type 3 thoracic)

Ramphastos sulfuratus brevicarinatus Gould (2) (Type 1 thoracic)

Ramphastos cuvieri Wagler (Type 1 or 2 thoracic)

Ramphastos tucanus Linné (Type 2 thoracic)

Ramphastos toco P. L. S. Müller (Type 2 thoracic)

Family PICIDAE

Carotids B–4–s, except for a specimen of *Piculus rubiginosus* (B–3a–d); type A coracoid; type 3 thoracic artery; presence of a ligamentum botalli variable; origin of vertebrals and superficial cervicals variable, but are usually in close association; an accessory oesophageal artery arises as a branch of the left carotid, or from the left superficial cervical artery; in several species, a pair of vessels supplying the trachea and syrinx arises as a branch from the common carotid artery near its base.

SPECIES STUDIED

By Garrod

Jynx torquilla Linné

Chloronerpes yucatanensis=*Piculus rubiginosus yucatanensis* (Cabot)

Gecinus viridis=*Gecinulus viridis* Blyth

Mulleripicus fulvus (Quoy and Gaimard)

Tiga javensis=*Dryocopus javensis* (Horsfield)

Melanerpes formicivorus (Swainson)

Leuconerpes candidus (Otto)

Picus major=*Dendrocopos major* (Linné)

Picus minor=*Dencrocopos minor* (Linné)

Picoïdes tridactylus (Linné)

By Glenny

Picumnus pumilus Cabanis and Heine

Picumnus cirratus pilcomayensis Hargitt

Picumnus squamulatus röhli Zimmer and Phelps

Nesoctites micromegas (Sundevall)

Colaptes cafer collaris Vigors

Colaptes auratus luteus Bangs

Colaptes auratus chrysocaulosus Grundlach

Colaptes pitius (Molina)

Colaptes campestris campestroïdes (Malherbe)

Nesoceleus fernandinae (Vigors)

Chrysoptilus melanochloros nigroviridis C. Grant

Piculus rubiginosus (Swainson) (B–3a–d)

Piculus rubiginosus tucumanus (Cabanis)

Piculus flavigula (Boddaert)

Piculus chrysochloros (Vieillot)

Campethera permista (Reichenow)
Celeus flavescens kerri Hargitt
Celeus flavus (P. L. S. Müller)
Picus canus zimmermanni Reichenow
Picus canus dedemi (van Oort)
Dinopium benghalense erythronothon (Vieillot)
Dryocopus javensis parvus (Richmond)
Dryocopus pileatus (Linné)
Asyndesmus lewis (G. R. Gray)
Melanerpes hypopolius uropygialis (Baird)
Melanerpes carolinus (Linné) (2)
Melanerpes superciliaris (Temminck)
Melanerpes striatus (P. L. S. Müller)
Melanerpes pucherani (Malherbe)
Melanerpes rubricapillus terricolor (Berlepsch)
Melanerpes cruentatus (Boddaert)
Leuconerpes candidus (Otto)
Sphyrapicus varius ruber (Gmelin)
Sphyrapicus varius (Linné)
Sphyrapicus thyroideus (Cassin)
Trichopicus cactorum (d'Orbigny)
Veniliornis spilogaster (Wagler)
Veniliornis passerinus olivinus (Natterer and Malherbe)
Veniliornis frontalis (Cabanis)
Veniliornis kirkii cecilii (Malherbe)
Dendrocopos villosus villosus (Linné) (3)
Dendrocopos villosus audubonii (Swainson)
Dendrocopos pubescens medianus (Swainson) (3)
Dendrocopos borealis (Vieillot) (2)
Picoïdes tridactylus dorsalis Baird
Picoïdes arcticus (Swainson)
Xiphidiopicus percussus (Temminck)
Phloeoceastes melanoleucos malherbii (G. R. Gray)
Phloeoceastes melanoleucos (Gmelin)
Phloeoceastes leucopogon (Valenciennes) (3)
Campephilus principalis (Linné)

Order PASSERIFORMES

Carotids B–4–s except for *Orthonyx*, which is said (Beddard, 1898) to be B–5–s; coracoid artery varies, but is usually type A; thoracic artery varies, but type 3 and type 4 are the most common; ligamentum aortae is present in most of the families, but this is somewhat variable and may not be detected due, perhaps, to the amount or level of atrophy; ligamentum botalli usually absent or reduced to a linea botalli; vertebrals and superficial cervicals vary in points of origin from the common carotids; an accessory oesophageal artery arises as a branch of the common carotid or one of the cervical arteries of the left side, when present.

It is difficult to determine the presence of the latter vessel in specimens that have been preserved for some time and as a result may be overlooked.

References: Bauer, 1825; Beddard, 1898; Biswas, 1946; Garrod, 1873; Glenny, 1940a, 1942a, 1944f, 1945a, 1945f, 1951b; Meckel, 1826; Stresemann, 1927–1934.

Family Eurylaimidae

No information available.

Family Dendrocolaptidae

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae present but reduced; vertebrals and superficial cervicals usually have a common root.

SPECIES STUDIED

By Glenny

Sittasomus griseicapillus griseus Jardine
Xiphorhynchus picus choicus (Wetmore and Phelps)
Xiphorhynchus triangularis hylodromus Wetmore
Lepidocolaptes souleyetii littoralis (Hartert and Goodson)
Campylorhamphus trochilirostris venezuelensis (Chapman)

Family FURNARIIDAE

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae small but usually present; vertebrals and superficial cervicals may have a short common root or arise separately.

SPECIES STUDIED

By Glenny

Cranioleuca subcristata (Sclater)
Anabacerthia striaticollis venezuelana (Hellmayr)
Phylidor rufus columbianus Cabanis and Heine
Xenops rutilans heterurus Cabanis and Heine

Family FORMICARIIDAE

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae present; vertebrals and superficial cervicals arise separately, or have but a short common root; the ascending oesophageal artery (right side) is usually prominent.

SPECIES STUDIED

By Glenny

Dysithamnus mentalis cumbreanus Hellmayr and Seilern
Dysithamnus plumbeus tucuyensis Hartert
Myrmotherula schisticolor sanctae-martae Allen
Drymophila caudata klagesi Hellmayr and Seilern
Formicarius analis saturatus Ridgway
Formicarius nigricapillus Ridgway

Family CONOPOPHAGIDAE

No information available.

Family RHINOCRYPTIDAE

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae present; vertebrals and superficial cervicals arise from a common, short root or separately from the common carotid artery; the ascending oesophageal artery of the right side is prominent.

SPECIES STUDIED

By Garrod	By Glenny
Hylactes megapodius = *Pteroptochos megapodius* Kittlitz	*Pteroptochos* sp.

Family COTINGIDAE

Type A coracoid, except in *Tityra inquisitor* (type D); type 1 thoracic artery; ligamentum aortae present; ligamentum botalli present in a specimen of *Pyroderus scutatus*, which also presented two pairs of superficial cervical arteries, and an accessory oesophageal artery arising as a branch of the secondary or ventral superficial cervical artery of the left side; vertebrals and superficial cervicals have a short common root from the common carotid.

A specimen of *Lipaugus cineraceus* was found to be type A coracoid artery and type 3 thoracic artery.

SPECIES STUDIED

By Garrod

Lipaugus cineraceus (Vieillot)
Rupicola crocea = *Rupicola rupicola* (Linné)
Pachyramphus albogriseus Sclater
Tityra inquisitor (Lichtenstein)
Pyroderus scutatus (Shaw)
Procnias nudicollis (Vieillot)

By Glenny

Lipaugus cineraceus (Vieillot)

Family PIPRIDAE

Type A coracoid artery; type 3 or type 4 thoracic artery; vertebrals and superficial cervicals arise separately, or from a short, common root; ligamentum aortae may be absent.

SPECIES STUDIED

By Glenny

Pipra pipra anthracina Ridgway

Family TYRANNIDAE

Type A coracoid artery; type 3 or more rarely type 4 thoracic artery; ligamentum aortae present; vertebrals and superficial cervicals arise as branches of a common root from the common carotid; the right carotid sends off an ascending oesophageal artery.

SPECIES STUDIED

By Garrod

Tyrannus satrapa = *Tyrannus melancholicus* Vieillot
Pitangus sulphuratus (Vieillot)

By Glenny

Xolmis cinerea (Vieillot)
Xolmis murina (Lafresnaye and d'Orbigny)
Xolmis rubetra (Burmeister)
Pyrocephalus rubinus dubius Gould
Muscivora forficata (Gmelin)
Tyrannus tyrannus (Linné) (2)
Tyrannus vociferans Swainson
Tyrannus melancholicus Vieillot (2)
Tyrannus dominicensis (Gmelin)
Pitangus sulphuratus derbianus (Kaup)
Myiarchus crinitus (Linné)
Eribates magnirostris (Gould)
Empidonax virescens (Vieillot)
Empidonax traillii (Audubon)
Myiophobus fasciatus (P. L. S. Müller)
Todirostrum cinereum (Linné)
Pogonotriccus ophthalmicus Taczanowski
Pogonotriccus venezuelanus Berlepsch
Pogonotriccus flaviventris (Hartert)

Families Oxyruncidae and Phytotomidae

No information available.

Family Pittidae

Type B coracoid artery; type 1 thoracic artery; ligamentum aortae present; vertebrals and superficial cervicals have a short, common root from the common carotid; the right common carotid sends off an ascending oesophageal artery.

Species studied

By Garrod

Pitta sp.

By Glenny

Pitta erythrogaster Temminck

Families Acanthisittidae and Philepittidae

No information available.

Family Menuridae

No details available.

Species studied

By Garrod

Menura superba Davies

Family Atrichornithidae

No information available.

Family Alaudidae

No details available.

Species studied

By Garrod

Alauda arvensis Linné
Melanocorypha calandra (Linné)

Family HIRUNDINIDAE

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae usually present but reduced; vertebrals and superficial cervicals usually arise as branches from a common root; an ascending oesophageal artery arises as a branch from the right common carotid artery.

SPECIES STUDIED

By Garrod	By Glenny
Hirundo rustica Linné	*Progne subis* (Linné)
Chelidon urbica=*Hirundo urbica* Linné	*Hirundo rustica erythrogaster* Boddaert
	Phaeoprogne tapera (Linné)

Family CAMPEPHAGIDAE

No details available.

SPECIES STUDIED

By Garrod

Graucalus macei Lesson

Family DICRURIDAE

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae present; vertebral and superficial cervical arteries have a common root from the common carotid artery; the ascending oesophageal artery arises as a branch of the right common carotid artery.

SPECIES STUDIED

By Garrod	By Glenny
Dicrurus leucops Wallace	*Dicrurus ater cathoecus* (Swinhoe)

Family ORIOLIDAE

Type A coracoid artery; types 1 to 4 thoracic artery; ligamentum aortae present; vertebrals and superficial cervicals have a common root from the common carotids; ascending oesophageal artery arises as a branch of the right common carotid artery.

SPECIES STUDIED

By Garrod	By Glenny
Oriolus sp.	*Oriolus xanthornus* Linné
	Oriolus chinensis diffusus Sharpe

Family Corvidae

Type A coracoid artery; types 1 to 4 thoracic artery; ligamentum aortae present; vertebrals and superficial cervicals arise from a common root from the common carotid arteries; ascending oesophageal artery arises as a branch of the right common carotid artery.

Species studied

By Garrod

Cissa speciosa=*Cissa chinensis* Boddaert
Cyanocorax cyanopogon (Wied)
Garrulus glandarius (Linné)
Corvus corax Linné
Corvus frugilegus Linné
Corvus australis Gmelin
Struthidea cinerea Gould

By Glenny

Corvus brachyrhynchos Brehm
Coloeus monedula dauuricus (Pallas) (2)
Cyanopica cyanus interopsita Hartert
Cyanocitta cristata bromia Oberholser
Xanthoura yncas (Boddaert)
Perisoreus canadensis (Linné) (2)

Families Cracticidae and Grallinidae

No information available.

Family Ptilonorhynchidae

No details available.

Species studied

By Garrod

Ptilonorhynchus holosericeus=*Ptilonorhynchus violaceus* (Vieillot)

Families Paradiseidae and Paradoxornithidae

No information available.

Family Paridae

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae present but reduced; vertebrals and superficial cervicals arise separately or as branches of a short common root from the common carotids; ascending oesophageal artery arises as a branch of the right common carotid artery.

Species studied

By Garrod

Parus major Linné

By Glenny

Parus atricapillus (Linné) (2)
Parus bicolor (Linné) (3)
Parus palustris hellmayri (Bianchi)
Parus major artatus Thayer and Bangs

Family Sittidae

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae usually present but reduced; vertebrals and superficial cervicals may arise separately or from a short common root from the common carotid arteries; ascending oesophageal artery arises as a branch of the right common carotid artery.

SPECIES STUDIED

By Garrod	By Glenny
Sitta europaea Linné	*Sitta carolinensis* Latham (2)

Family HYPOSITTIDAE

No information available.

Family CERTHIIDAE

Type A coracoid artery; types 3 and 4 thoracic artery; ligamentum aortae much reduced; vertebrals and superficial cervicals arise separately or from a short common root from the common carotids; ascending oesophageal artery arises as a branch of the right common carotid artery.

SPECIES STUDIED

By Glenny

Certhia familiaris americana (Bonaparte)

Families CHAMAEIDAE AND TIMALIIDAE

No information available.

Family PYCNONOTIDAE

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae not observed; vertebrals arise separately from superficial cervicals or from a short root from the common carotids; ascending oesophageal artery arises as a branch of the right common carotid artery.

SPECIES STUDIED

By Glenny

Aegithina tiphia zelonica (Gmelin) | *Chlorocichla flaviventris* (Smith)

Family CINCLIDAE

No details available.

SPECIES STUDIED

By Garrod

Cinclus aquaticus = *Cinclus cinclus aquaticus* Bechstein

Family TROGLODYTIDAE

Type A coracoid artery; types 3 or 4 thoracic artery; ligamentum aortae greatly reduced or lacking; vertebrals and superficial cervicals arise from a common root from the common carotid arteries; ascending oesophageal artery arises as a branch from the right common carotid artery.

SPECIES STUDIED

By Garrod	By Glenny
Troglodytes parvulus=*Troglodytes troglodytes* (Linné)	*Troglodytes aëdon* Vieillot (2)
	Telmatodytes palustris Wilson
	Thryothorus genibarbis Swainson

Family MIMIDAE

Type A coracoid artery; types 3 or 4 thoracic artery; ligamentum aortae much reduced or absent; vertebrals and superficial cervicals arise from a short common root from the common carotid artery; ascending oesophageal artery arises as a branch of the right common carotid artery.

SPECIES STUDIED

By Glenny

Toxostoma rufum (Linné)

Family TURDIDAE

Type A coracoid artery; types 3 and 4 thoracic artery; ligamentum aortae reduced or absent; vertebrals and superficial cervicals arise as branches of a common root from the common carotid artery; ascending oesophageal artery arises as a branch of the right common carotid artery.

SPECIES STUDIED

By Garrod	By Glenny
Sialia wilsonii=*Sialia sialis* (Linné)	*Sialia sialis* (Linné)
Turdus grayi Bonaparte	*Turdus migratorius* Linné
Myiadestes obscurus Lafresnaye	*Hylocichla ustulata swainsoni* (Cabanis) (2)
Turdus merula Linné	*Hylocichla minima minima* (Lafresnaye)
Pratincola rubetra (Linné)	*Hylocichla guttata pallasi* (Cabanis)
Ruticilla phoenicura=*Phoenicurus phoenicurus* (Linné)	*Hylocichla mustelina* (Gmelin)
Erithacus rubecula (Linné)	
Luscinia vera=*Luscinia megarhynchos* Brehm	

Family ZELEDONIIDAE

No information available.

Family SYLVIIDAE

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae reduced; vertebrals and superficial cervicals arise as branches of a common root from the common carotid arteries; ascending oesophageal artery arises as a branch of the right common carotid artery.

SPECIES STUDIED

By Garrod	By Glenny
Anthornis melanura=*Polioptila melanura* Lawrence	*Polioptila plumbea* (Gmelin)
Sylvia hippolais=*Hippolais icterina* (Vieillot)	*Polioptila caerulea* Linné

Family REGULIDAE

Type A coracoid artery; type 3 or 4 thoracic artery; ligamentum aortae not observed; vertebrals and superficial cervicals arise from a common root from the common carotid artery; ascending oesophageal artery arises as a branch of the right common carotid artery.

SPECIES STUDIED

By Glenny

Regulus satrapa Lichtenstein

Family MUSCICAPIDAE

No details available.

SPECIES STUDIED

By Garrod

Muscicapa grisola=*Muscicapa striata* (Pallas)

Family PRUNELLIDAE

No information available.

Family MOTACILLIDAE

Type A coracoid artery; types 3 and 4 thoracic artery; ligamentum aortae not observed; vertebrals and superficial cervicals arise from a common root from the common carotid artery; ascending oesophageal artery arises as a branch of the right common carotid artery.

SPECIES STUDIED

By Garrod	By Glenny
Anthus pratensis (Linné)	*Anthus spinoletta rubescens* (Tunstall)
Motacilla flava Linné	

Family BOMBYCILLIDAE

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae present; vertebrals and superficial cervicals arise as branches from a common root from the common carotid artery; a pair of ascending oesophageal arteries were observed to arise as branches of the common carotid arteries.

Species studied

By Garrod	By Glenny
Ampelis garrulus=*Bombycilla garrulus* (Linné)	*Bombycilla cedrórum* Vieillot

Family Ptilogonatidae

No details available.

Species studied

By Garrod

Ptilogonys cinereus Swainson

Family Dulidae

No information available.

Family Artamidae

No details available.

Species studied

By Garrod

Artamus sp.

Family Vangidae

No information available.

Family Laniidae

No details available.

Species studied

By Garrod

Lanius collurio Linné

Strepera graculina (White)

Family Prionopidae

No details available.

Species studied

By Garrod

Sigmodus caniceps Bonaparte.

Families Cyclarhidae, Vireolaniidae, and Callaeidae

No information available.

Family Sturnidae

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae reduced or absent; ligamentum botalli observed in *Aplonis tabuensis;* vertebrals and superficial cervicals arise as branches of a common root from the common carotids; ascending oesophageal artery arises as a branch of the right common carotid artery.

Species studied

By Garrod	By Glenny
Sturnus vulgaris Linné	*Sturnus vulgaris* Linné
Heteralocha gouldi=*Heteralocha acutirostris* (Gould)	*Aplonis tabuensis* (Gmelin)
Gracula religiosa (Linné)	

Family Meliphagidae

No details available.

Species studied

By Garrod

Tropidorhynchus sp. | *Posthemadera novae-zealandiae* (Gmelin)

Family Nectariniidae

No details available.

Species studied

By Garrod

Nectarinia sp.

Family Dicaeidae

No details available.

Species studied

By Garrod

Dicaeum sp.

Family Zosteropidae

No details available.

Species studied

By Garrod

Zosterops albogularis=*Zosterops albigularis* Gould.

Family Vireonidae

Type A coracoid artery; types 3 and 4 thoracic artery; ligamentum aortae reduced; vertebrals and superficial cervicals arise from a short common root from the common carotid arteries; ascending oesophageal artery arises as a branch of the right common carotid artery.

Species studied

By Glenny

Vireo solitarius (Wilson) | *Vireo virescens* Vieillot

Family Coerebidae

Type A coracoid artery; type 4 thoracic artery; ligamentum aortae reduced; vertebrals and superficial cervicals arise as branches of a common root from the common carotid arteries; ascending oesophageal artery arises as a branch of the right common carotid artery.

Species studied

By Garrod

Coereba cyanea = *Cyanerpes cyaneus* (Linné)
Diglossa baritula Wagler

By Glenny

Cyanerpes caeruleus (Linné) (3)

Family Drepanididae

No information available.

Family Parulidae

Type A coracoid artery; types 3 and 4 thoracic artery; ligamentum aortae reduced or absent; vertebrals and superficial cervicals arise from a common root from the common carotid arteries; ascending oesophageal artery arises as a branch of the right common carotid artery.

Species studied

By Garrod

Mniotilta varia (Linné)

By Glenny

Protonotaria citrea (Boddaert)
Vermivora peregrina (Wilson)
Vermivora ruficapilla (Wilson)
Dendroica coronata (Linné)
Dendroica cerulea (Wilson)
Dendroica fusca (Müller)
Dendroica breviunguis (Spix)
Seiurus aurocapillus (Linné)
Seiurus noveboracensis (Vieillot)
Oporornis formosus (Wilson)
Geothlypis trichas (Linné)
Setophaga ruticilla (Linné) (2)
Myioborus miniatus (Swainson)
Basileuterus tristriatus (Tschudi)
Basileuterus culicivorus (Lichtenstein)

Family Ploceidae

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae reduced; vertebrals and superficial cervicals arise as branches of a common root from the common carotid artery; ascending oesophageal artery arises as a branch of the right common carotid artery

In a single specimen of *Ploceus p. philippinus*, both left and right systemic arches and radices aortae were present, as well as the right and left ligamenti botalli (Biswas 1946).

Species studied

By Biswas

Ploceus philippinus philippinus (Linné)

By Garrod

Ploceus manyar (Horsfield)
Poephila cincta (Gould)
Munia major = *Munia maja* (Linné)
Euplectes capensis (Linné)
Estrelda melpoda = *Sporaeginthus melpodus* (Vieillot)
Hyphantornis castaneo-fuscus = *Melanopteryx castaneofusca* (Lesson)
Padda oryzivora = *Munia oryzivora* (Linné)
Donacola castaneothorax = *Munia castaneothorax* (Gould)
Quelea occidentalis = *Quelea quelea quelea* Linné

By Glenny

Passer domesticus Linné (2)
Passer montanus saturatus (Stejneger)

Family Icteridae

Type A coracoid artery; types 3 and 4 thoracic artery; ligamentum aortae much reduced or absent; vertebrals and superficial cervicals arise as branches of a common root from the common carotids; ascending oesophageal artery arises as a branch of the right common carotid artery.

Species studied

By Garrod

- *Cassicus persicus*=*Cacicus vitellinus* Lawrence
- *Agelaeus ludovicianus*=?*Sturnella magna* (Linné)
- *Icterus abeillei* (Lesson)
- *Molothrus bonariensis*=*Molothrus bonariensis atronitens* (Cabanis)

By Glenny

- *Xanthornus angustifrons* (Spix)
- *Molothrus ater* (Boddaert)
- *Ptiloxena atroviolacea* (d'Orbigny)
- *Icterus galbula* (Linné)
- *Icterus dominicensis* (Linné)
- *Agelaius phoeniceus* (Linné)

Family Tersinidae

No information available.

Family Thraupidae

Type A coracoid artery; type 3 thoracic artery; ligamentum aortae somewhat reduced or lacking; vertebrals and superficial cervicals arise as branches from a common root from the common carotids; ascending oesophageal artery arises as a branch of the right common carotid artery.

Species studied

By Garrod

- *Euphonia violacea*=*Tanagra violacea* (Linné)
- *Tanagra cana*=*Thraupis episcopus cana* (Swainson)
- *Cissopis leveriana* (Gmelin)

By Glenny

- *Calospiza chrysophrys* (Sclater)
- *Calospiza arthus* (Lesson)
- *Calospiza gyrola* (Linné)
- *Compsocoma flavinucha* (Lafresnaye and d'Orbigny)
- *Thraupis episcopus* (Linné)
- *Thraupis palmarum* (Wied)
- *Thraupis cyanocephala* (Lafresnaye and d'Orbigny)
- *Ramphocelus carbo* (Pallas)
- *Ramphocelus dimidiatus isthmicus* Ridgway
- *Tachyphonus rufus* (Boddaert)

Family Catamblyrhynchidae

No information available.

Family Fringillidae

Type A coracoid artery; type 3 thoracic artery, but type 4 may also be present occasionally; ligamentum aortae usually present; ligamentum botalli rarely present; vertebrals and superficial cervicals arise from a common root from the common carotid arteries; ascending oesophageal artery arises as a branch of the right common carotid artery.

SPECIES STUDIED

By Garrod

Coccothraustes vulgaris=*Coccothraustes coccothraustes* (Linné)
Hedymeles ludoviciana=*Pheucticus ludovicianus* (Linné)
Cardinalis virginianus=*Richmondena cardinalis* (Linné)
Corythus enucleator=*Pinicola enucleator* (Linné)
Cyanospiza ciris=*Passerina ciris* (Linné)
Emberiza sp.
Liniaria cannabina (Linné)
Pyrrhula vulgaris=*Pyrrhula pyrrhula europaea* Vieillot

By Glenny

Geospiza fuliginosa Gould
Geospiza septentrionalis (Rothschild and Hartert)
Certhidea olivacea cinerascens Ridgway
Pheucticus ludovicianus (Linné)
Guiraca caerulea (Linné)
Loxigilla violacea affinis (Baird)
Loxigilla noctis sclateri (Allen)
Loxipasser anoxanthus (Gosse)
Sporophila aurita (Bonaparte)
Tiaris olivacea (Linné)
Tiaris bicolor omissa Jardine
Melopyrrha nigra (Linné)
Amaurospiza concolor Cabanis
Richmondena cardinalis (Linné)
Saltator albicollis isthmicus (Sclater)
Fringilla coelebs Linné
Fringilla montifringilla Linné
Hesperiphona vespertina (W. Cooper)
Serinus canaria (Linné)
Pyrrhula pyrrhula (Linné)
Melospiza melodia (Wilson)
Pinicola enucleator leucura (Müller) (2)
Leucosticte tephrocotis griseonucha (Brandt)
Carduelis carduelis (Linné)
Acanthis flammea (Linné)
Spinus tristis (Linné)
Coryphospingus pileatus (Wied)
Arremonops conirostris (Bonaparte)
Pipilo erythrophthalmus (Linné)
Pipilo fuscus mesoleucus Baird (2)
Passerculus sandwichensis savanna (Wilson)
Junco hyemalis (Linné)
Spizella arborea (Wilson) (2)
Spizella passerina (Bechstein)
Spizella pusilla (Wilson)
Zonotrichia albicollis (Gmelin)
Passerella iliaca (Merrem)
Emberiza flaviventris Stephens
Emberiza aureola Pallas
Paroaria capitata (Lafresnaye and d'Orbigny)

Paramorphogenesis in the aortic arch system

Paramorphogenesis is, quite simply, parallel structural development and evolution. The term can be applied when structures are homologous, and when developmental evolution of a structure follows the same pattern and general course of events to arrive at the same or similar end insofar as structure is concerned. This term should be applied only when such patterns of structural evolution occur in distantly related forms, as in orders and classes of organisms, and when there is no apparent link or graded series leading from some known ancestral form to its present-day descendents in any of several different orders.

Paramorphogenesis is not to be confused with the term convergence; rather, it implies a general tendency toward structural evolution along the same or similar lines in separate or diverse groups of allied forms, especially those forms which are presumed to be related—as orders and classes of vertebrates, especially as in the amniotes.

All birds, insofar as presently known, develop a complete aortic arch system, and this system undergoes a series of developmental (atrophic) deletions and other modifications which result in the adult arterial arrangement-patterns, most of which have been set forth in the previous chapter. It is now a question as to whether the fourth and fifth aortic arches make an appearance in at least several of the Trochilidae, and, if they do, for what period of time they are present. Glenny (1953b, 1954c) has shown that the right systemic arch may be absent in several species of hummingbirds, and that the ductus caroticus serves the function of the fourth arch in these instances.

That widely separated orders of birds should undergo similar evolutionary changes in the aortic arch system is in itself a fact worthy of note, but that a somewhat similar instance of deletion of the dorsal carotid should occur in *Alligator mississippiensis* is of still greater interest (Reese, 1914), especially in view of the fact that some zoologists have linked the Crocodilia and Aves to the same basic reptilian stem (Archosauria). In the alligator, the left dorsal carotid remains as the functional vessel and, as in most birds, this vessel enters the hypapophysial canal and passes anteriorly to the head where it sends off left and right branches which then further divide and supply the various parts of the cranial region. Thus the carotid arrangement in the alligator would be referred to as laevocarotidinae, and, as has already been demonstrated, this arrangement is quite common among the present-day birds.

Within the class Aves there is abundant evidence to show that evolution of the aortic arch system is still in progress, and that culmination of this evolution may be the complete loss of the dorsal carotids anterior to the carotid arch. In such instances where this condition has been found, the vertebrals and the superficial cervicals take over the function of supplying blood to the head.

Reduction and loss of the dorsal carotids may take place either by a series of microdeletions or by macrodeletion. Two known instances of the latter are found in *Bucorvus abyssinicus* and *Rhopodytes viridirostris,* while a macrodeletion of but one dorsal carotid is known to occur in *Rhamphococcyx curvirostris erythrognathus.* Such unilateral macrodeletions may be of more frequent occurrence than is known at present, and further studies of the aortic arch system in birds may reveal still other instances of bilateral atrophy and deletion of the dorsal carotids. These instances of carotid atrophy have been found to occur in the Coraciiformes and the Cuculiformes. The macrodeletions mentioned above were found in normally bicarotid (A–1) forms.

Evolution of the aortic arch system from a bicarotid to a unicarotid condition is of interest when considering the implications of paramorphogenesis. Presumably, for the most part, the two dorsal carotids become conjugate vessels. This is followed by reduction and ultimate loss of the basal portion of either the left or right side, and the functional adult condition is either dextrocarotidinae or laevocarotidinae, respectively.

The level of ordinal evolution may be inferred by the level of evolution of the dorsal carotids, at least insofar as the members of the order are concerned. Within an order or family in which partial or complete loss of one of the dorsal carotids has occurred, some estimate of the relative level of evolution of the species may be made. A graded series in the levels of atrophic evolution of the dorsal carotid arteries can be observed in several orders of birds (fig. 119).

In the macroevolution of the dorsal carotids the levels of evolution are quite simplified, but in the microevolution of these same vessels there are several important steps in the reduction and ultimate deletion of a vessel.

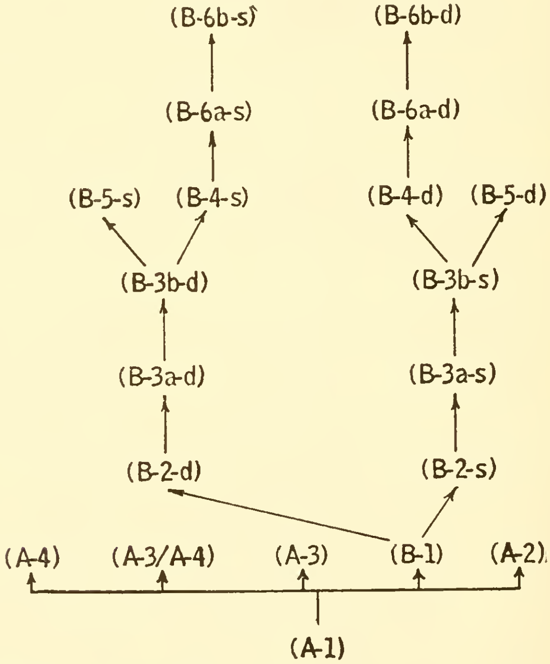

Figure 119.—Graded series or levels in the evolution of the dorsal carotid arteries in birds.

The following orders and families, in which there is evidence of some carotid artery evolution, are listed according to the carotid arrangements reported for each group. Orders and families of birds not included in this list either are bicarotidinae normales (A–1) or the condition of the carotid arrangement has not been established.

Orders

B–4–s

Rheiformes
Apterygiformes
Colymbiformes
Coliiformes
Trogoniformes
Piciformes, with a single case of B–4–d
Passeriformes except in *Orthonyx*, B–5–s

Families and subfamilies

B–4–s

Anhingidae
Balaenicipitidae
Turnicidae
Nyctibiidae
Hemiprocnidae
Trochilidae
Upupidae
Phoeniculidae

A–1, A–2–s

Loriinae
Psittacinae

A–2–s

Nestorinae

A–1, A–3

Cuculidae

A–1, A–4

Cuculidae
Bucerotidae

A–1, A–3–s/A–4–d

Cuculidae

A–1, B–1, B–2–s

Ardeidae

A–1, B–2–s

Kakatoeinae

B–2–s

Phoenicopteridae
Megapodidae

A–1, B–2–d, B–3b–d

Kakatoeinae

A–1, B–3a–d

Procellariidae
Bucerotidae

A–1, B–3b–d, B–4–s

Apodidae

B–2–d, B–4–s

Podargidae

B–3b–d

Pelecanidae

B–3b–d, B–4–s

Megapodidae

A–1, B–4–d

Otidae

A–1, B–4–s

Casuariidae
Pelecanoididae
Sulidae
Fregatidae
Alcidae
Meropidae

It will be noted in the above list that, for the most part, there is a major trend toward deletion of the right dorsal carotid artery. In the Ciconiiformes, however, the trend is more generally in the direction of a dextral evolution and deletion of the left carotid artery. This can be observed in both the Ardeidae and the Phoenicopteridae. *Balaeniceps rex*, on the other hand, has evolved along the sinistral course.

Retention of the bicarotidinae normales (A–1) arrangement should be regarded as a more basic condition with respect to the evolution of the carotid arteries.

It is felt that from the above information sufficient evidence has been presented to demonstrate a high degree of paramorphogenesis in the aortic arch system of birds.

Discussion and conclusions

The arrangement of the thoracic and cervical derivatives of the aortic arch system—especially the branches of the subclavian and pectoral stem arteries—in the ostrich, rhea, and cassowary clearly substantiates the view that these forms are secondarily modified and are not extant species derived from holocursorial ancestors. In the kiwi, on the other hand, the arrangement and supply of the arteries can hardly be interpreted as having been derived from an ancestor possessing the normal flight-function, although a volant ancestor cannot be excluded from their line of evolution.

Carotid evolution of the Colymbiformes is such as to indicate a considerable advance over the bicarotid ancestral forms, and the wide distribution of species of this order tends to further substantiate the view that the origin of this order of birds occurred early in avian history. A similar interpretation may be made for the very early origin of the kiwis.

The dextral evolution of the carotids in both the Ardeidae and Phoenicopteridae tends to further indicate the affinities of the flamingos with the herons rather than with the ducks, which are altogether bicarotidinae normales. In addition, the laevocarotid arrangement in *Balaeniceps rex* is further evidence for its singular position among the Ciconiiformes, and warrants its allocation to a separate family (Balaenicipidae).

Affinities between the tinamous and gallinaceous birds are apparent, but close and recent relationships can hardly be substantiated. While these two orders may well have had a very early, common origin, most of the gallinaceous birds have evolved along many more diverse lines of specialization than has been the case among the tinamous.

In discussing the generic relationships of the parrots, Amadon (1942) has pointed out that Latham considered *Prosopeia tabuensis* and *Alisterus scapularis* to be varieties of one species. This I cannot properly ascribe to, since two subspecies of *Prosopeia tabuensis* were found to have the A–2–s carotid arrangement while *Alisterus scapularis* has the A–1 carotid arrangement and is more closely allied with *Polytelis,* but not with *Cyanoramphus* or *Platycercus.* Both of these latter genera show closer affinities with *Prosopeia* in that they all present the A–2–s carotid arrangement. The platycercine lack a furcula, as they have class 3 clavicles (Glenny, 1954b). Among the Psittacinae, it is my opinion that the A–2–s forms are more closely related by way of some common ancestral form than as a result of the comingled relationship with A–1 carotid types. It is suggested that the species *Lathamus discolor* be completely reexamined to determine its exact relationships, for it may well be a monotypic form, not properly placed among the Loriinae, since the carotid arrangement is of the A–2–s type, while all other members of this subfamily, thus far examined, have the A–1 carotid arrangement. Other similarities to the Loriinae may be instances of paramorphogenesis and, as a relict evolutant, it may constitute a monotypic subfamily, or be reassigned to the Psittacinae.

Certain phyletic relationships may be ascertained reasonably well on the basis of the carotid artery arrangement, and the arterial arrangement-patterns appear to have a phylogenetic significance. The constancy of occurrence of the basic bicarotid condition and the progressive developmental steps that lead to several modifications of the system tend to point to this conclusion and to substantiate, in part, the theory that ontogeny recapitulates phylogeny.

As a result of early dispersal movements of birds and mammals from their center(s) of origin, a large number of fossil forms might well be expected in many parts of the land areas. Few of these fossils can well be considered as true ancestral forms which led to the present-day species, but strong similarities in structure might show their affinities with extant species.

Occurrence of relict species and families of birds and mammals in Australia, New Zealand, and South America tends to support the view that birds and mammals may well have originated in Antarctica, and that as a result of protective isolation in these localities they were able to survive and undergo considerable speciation.

Evolution of both birds and mammals must have been from reptilian forms which had a reasonably well developed sternum, since this structure is found in both classes but is more highly developed in birds than in mammals. This tends to preclude any relationship between the Neornithes and the so-called Archaeornithes (*Archaeopteryx* and *Archaeornis*). Simpson (1946) has summarized Lowe's views with respect to *Archaeopteryx* and *Archaeornis:* In most respects they are purely reptilian, in all respects they are as reptilian as avian, and in some respects they are too specialized to be ancestral to birds. It is suggested, therefore, that the forms now placed in the Archaeornithes be placed in the Sauropsida with the Reptilia, since mere presence of feathers is not sufficient grounds for placing them in close association with modern birds and cannot be construed as sufficient evidence for a closer phyletic relationship. The presence of scales on birds and some mammals is as sound single evidence for placing both of these classes of vertebrates in the Sauropsida as the presence of feathers on reptiles is for placing them among the birds.

During the earliest stages of avian and mammalian evolution, a rapidly evolving group of profamily types probably took place, with the result that the predecessors for all major avian and mammalian groups might well have been developed. Subsequent to their origin and early radiation, further evolution of the major groups could have taken place in other and more widely separated areas with the resultant complex distribution of forms, both fossil and living.

On the assumption that evolution is greatly accelerated in a tropical climate and that the arboreal habit in a tropical climate tends to be predominant, it may be concluded that ancestral primates and ancestral marsupials were more or less contemporaries (Simpson, 1945), and that the eutherians were not evolved from the metatherians but that both groups have evolved independently and simultaneously along somewhat different and more specialized lines (Romer, 1945). The same view then may be taken with respect to the evolution of the major orders of birds. Thus, once the earliest avian ancestors had become established, the pro-order and perhaps even the profamily types probably developed quite rapidly and these may well have been contemporaries. Since the earliest beginnings of proavian forms there has been a notable degree of specialization of structures, feeding habits, and environmental adjustments resulting in the complex avian fauna as we know it today.

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