THE MORPHOLOGY OF THE MAMMALIAN CORACOID.

By G. B. HOWES, F.L.S., F.Z.S., *Assistant Professor of Zoology, Normal School of Science and Royal School of Mines, South Kensington.* (PLATE VIII.)

(Read before the British Association at Birmingham, September 1886.)

IT is generally accepted and taught that the shoulder-girdle of the didelphous and placental mammals is usually ossified from two centres, the resultant bones being the scapula and the coracoid process; and it is further customarily assumed that the latter is the serial homologue of the coracoid bar of the lower vertebrata.

While engaged some few years ago upon a detailed examination of the common rabbit, there came under my notice a third ossific centre herein to be described, the importance of which has since grown upon me. Krause makes no mention of it in his special treatise upon the Leporine.[1] My friend Professor T. J. Parker has done me the honour of incorporating the observation in his *Zootomy*,[2] describing the coracoid process of the rabbit (p. 278) as "consisting in the young animal of two separate ossifications, and representing the coracoid of the lower vertebrata." Sabatier[3] describes and figures it in the hare. Flower, writing of the mammalian coracoid generally, states[4] that it ossifies from one or more separate centres, but goes no further; neither his description nor that of Parker do full justice to the facts as they stand, and I hope to show that the interpretation offered by Sabatier is, so far as pertains to the coracoid process, untenable.

If the blade-bone of a six-weeks' rabbit be examined, it will be found to consist of three well-defined elements, viz., a large scapula with a well-developed spine and metacromion, a coracoid process of relatively considerable dimensions, and the third bone

[1] *Die Anatomie des Kaninchens*, 2nd ed., Leipzig, 1884.

[2] *Zootomy*, London, 1884.

[3] *Comparison des Ceintures et des Membres ant. et post. dans la série d. vertébrés*, Paris, 1880.

[4] *Osteology of the Mammalia*, new ed., p. 248, 1885.

(*co'*. fig. 2), now under consideration. Upon looking at the glenoid facet from within (fig. 3) it will be seen that the coracoid process (*co.'*) does not enter into any share of its formation; it is shut out by the third bone (*co.*), the exposed ventral surface of which is, together with that of the scapula, capped in cartilage. The new bone comes into existence during the third week of extra-terrestrial life, at a period when the coracoid process is nearing completion (fig. 1, *co.*, *co.'*); its duration as a separate element is exceedingly short, for, at about the sixth or seventh week it ankyloses with the adjacent centres to form the adult blade-bone. If the last-named structure be examined just prior to the ankylosis (fig. 2) the size and importance of the new element becomes very striking. It might be urged that it is an epiphysis, developed as a physiological necessity; but there is little demand for such in the case of a bone lying free as does this. It would further appear that it might answer to the "coracoid epiphysis" so well known to human anatomists;[1] but that view, if admitted, is no argument against the homology I am seeking to establish; in face of the fact that in the rabbit a small nucleus is occasionally present, related to it as it is to the human coracoid process, it decidedly supports me, as will be seen in the sequel. Moreover, the probability that it is a normal constituent of the shoulder-girdle appears to me to be greatly increased, upon reflection that we are now beginning to recognise in the cotyloid bone of the hip-girdle—a structure until quite recently regarded as an epiphysis—a new and important element.[2]

Assuming that the bone in question is one of regular occurrence among mammals, its homology has now to be considered. I am satisfied, as the result of examination of a series of specimens in each case, that it does not make its appearance in some two or three carnivores at least, and doubt not but that it is wanting in many other Monodelphs. I am equally satisfied that it is regularly developed in some few rodents. The conditions of its formation above recorded show that it is only to be found with some difficulty, and indicate that it must be searched for among placentals at a stage in the development later than those

[1] *Cf.* Humphry, *The Human Skeleton*, p. 368.
[2] *Cf.* Baur, *Zool. Anzeiger*, 1886, p. 107, footnote.

hitherto described in works classic. Our knowledge of the shoulder-girdle of the Didelphia does not help us much; from the small size of the coracoid process in the majority of these I suspect that it will be found to be obsolete, Phascolomys and Didelphys excepted (*cf.* Sabatier, *loc. cit.*, p. 75). The monotreme alone remains for comparison. The characters of the shoulder-girdle of the adult monotreme are too familiar to need description here; suffice it to say that it is usually held to differ from that of all other mammals, in the possession of a second coracoid element. Cuvier[1] first appreciated the real nature of this, and applied to it the term "epicoracoid" now in general use, as a substitute for the "clavicula coracoidea anterior" of Meckel.[2] Gegenbaur, writing[3] in 1865, describes it as an "eigenthumliche Bildung" which disappears in the higher mammals; regarding the latter he says (p. 3), "schwindet der dem Epicoracoid entsprechende Abschmitt vollstandig," and further, "immer verknochert auch der Processus coracoidës mit einem besonderen knochenkerne, der selbst vorhanden ist, wo der Fortsatz unansehnlich erscheint." These words embody the view predominant up to this present, but it is one which appears to me to be open to serious doubt. The shoulder-girdle of the Ornithodelph ossifies, as does that of the young rabbit, from three centres, viz., a dorsal scapula one and antero- and postero-ventral coracoid ones. The antero-ventral bone (epi-coracoid of the monotreme coracoid process of the higher Mammalia as here homologised) takes no share in the formation of the glenoid facet; it is, in both Monotreme and Leporine, inwardly directed, giving attachment wholly or in part to the biceps-brachii muscle.[4] The coracoid process of the higher mammalia is thus identical in its more important relationships with the epi-coracoid of the monotremes, and homologues I hold them to be; while the third bone, so well defined among rodents, answers with equal satisfaction to the coracoid bar of the monotreme and of the lower vertebrata. Should the above determination prove correct, it follows that the rabbit, with its

[1] *Leçons d'anat. comparée*, 2nd ed., vol. i. p. 356, 1835.

[2] *Ornithorhynchus paradoxus*, Leipzig, 1826.

[3] *Untersuchungen z. vergleichend. Anat. d. Wirbelth.*, pt. ii., Leipzig, 1865.

[4] *Cf.* Mivart, *Trans. Linn. Soc. Lond.*, vol. xxv. p. 386 *et seq.*, 1866; also Meckel, *op. cit.*

epi-coracoid and coracoid both shortened up, stands, in the mammalian series, midway between the monotreme in which the parts of the whole girdle are most uniformly developed and the higher placental, in which the coracoid process comes to enter into the formation of the glenoid facet in proportion as the coracoid bar is suppressed. The latter structure retires from the scene as the "coracoid epiphysis" of human anatomists.[1]

Comparison of the monotreme shoulder-girdle with that of the lower air-breathing vertebrata, suggests at first sight that fenestrated type so familiar in the Anura. Excluding the interclavicle, the two differ only in the absence in the former of the pre-coracoid cartilage; in other words, the mammalian shoulder-girdle, as represented in the monotremes, would appear to be derivative of a fenestrated type, the pre-coracoid element having disappeared. In the hope of testing this conception, it has been my good fortune to dissect the youngest monotreme girdle yet described. The specimen was that of a female Ornithorhynchus, having a total length of 9 inches.[2] Figs. 4 and 5 show how little the parts were ossified; the epi-coracoid (*co.'*) was entirely cartilaginous; the sternum was still a sheet, segmented only at its anterior end, and the ribs were for the most part confluent therewith. The second sternal segment (*st'.*) is remarkable for its precocious development; it was completely segmented off behind, and confluent marginally with the enormous omosternum (*st.*) in front. It was altogether more highly differentiated than any structure adjacent, and in it and the posterior pair of sternal ribs alone, among the sterno-costal apparatus, had ossification commenced (* fig. 4). The clavicular elements were fully formed and in place, the clavicle itself extending from the acromion (*a.*) (completely developed, but still cartilaginous) along the edge of the epi-coracoid; and assuming, as can barely be doubted, that the fenestra enclosed represents the coracoid fontanelle of the Amphibia, it was fair to expect

[1] I anticipate that a strict parallelism will be forthcoming between the steps in the suppression of this element in the Monodelphous and Didelphous groups. The probability of its being well developed in the Didelphyidæ is very suggestive of this.

[2] I am deeply indebted for the same to Professor W. K. Parker, F.R.S. The animal has been figured by him in his "Mammalian Descent," *College of Surgeon's Lectures*, p. 25, Feb. 1884.

that traces of the pre-coracoid cartilage should have been present. There was not a vestige of it. This fact, however, does not preclude the possibility of its previous existence, seeing that all who have studied the development of the mammalian clavicle are agreed that its ossification is effected at a stage antecedent to that of the rest of the girdle. That the clavicle of the Didelphia and Placentalia is regularly performed in cartilage there can no longer be a doubt. Rathke observed, nearly forty years ago,[1] that in those mammals possessed of a complete clavicle the entire shoulder-girdle arises as a continuous mass. Gegenbaur discovered,[2] some years later, that the human clavicle is preceded in cartilage, and he first fully elucidated the mode of development of the mammalian collar bone. He showed that while the cartilage becomes replaced in bone, the subsequent growth of the shaft takes place circumferentially, by the superaddition of periosteal bone, from which the main mass of the adult clavicle is derived. Consequent upon this, he modified the view then current, which regarded the clavicle as wholly a membrane bone. Failing, however, to find any indication of direct continuity between the cartilaginous clavicle and the acromion, he regarded the former as a super-added element, constituting no part of the primary shoulder-girdle. Goette, while endorsing, some years later, Gegenbaur's main discovery, sought to harmonise it with Rathke's statement already alluded to.[3] He, however, failed also to demonstrate that connection between the shoulder-girdle and the clavicular cartilage, the existence of which his conclusions presupposed. This was reserved for Hoffmann who, two years later, discovered,[4] in embryos of the three-toed sloth, direct continuity between the clavicle and the cartilaginous spine of the scapula, and, moreover, demonstrated (p. 37) a complete structural transition between them. He further described early stages in the development of the same

[1] *Ueb. die Entwickelung der Schildkröten*, p. 137, Brunswick, 1848.

[2] "Ein Fall v. erbblichem Mangel der Pars acromialis clavic. mit Bermerkungen u. d. Entwick. der clavic," *Jenaisch. Zeitschr.*, vol. i., 1864; also *op. cit.*, pp. 5-11. In the former communication (pp. 11-12) the growth of the clavicle is likened to that of a long bone.

[3] Primarily in his classic, "Die Entwickelungsgesch. d. Unke," pp. 616-19. Finally, in his "Beitr. z. vergl. Morphologie des Skeletsyst. der Wirbelth," *Archiv. f. Mikr. Anat.*, vol. xiv., 1877.

[4] "Beitr. z. vergl. Anat. d. Wirbelth," *Niederländ. Archiv.*, vol. v., 1879.

parts in the armadillo and other mammals (*cf.*, especially pl. 3, fig. 6), all of which unmistakably support Rathke's original assertion; his observation is the more welcome, so far as concern the sloths, in the light of views accepted to-day,[1] of their systematic position and structural lowliness.

Mivart has shown[2] that the doubts which have been thrown upon the homology of the monotreme processus-acromialis are unfounded; he has adduced, as the result of careful study of the muscular attachments, evidence conclusive of its identity with the spine of the scapula. This being so, comparison of the monotreme girdle with that of the amphibian, reveals, in the light of Hoffmann's discovery, a complete identity between the pre-coracoid cartilage of the adult Anuran and the cartilaginous clavicle of the embryo Mammal. The matter presses still more closely upon consideration of the precise mode of development of the clavicle, the periosteal constituent of which "anfangs eine Seite des Knorpels freilasst" in man himself (Goette, *loc. cit.*, p. 559). In the mammalia the bony clavicle, elevated (monotremes) as the result of development of the processus acromialis, becomes (placentalia) rotated outwardly and downwardly with the development of the pre-scapular lamina, and hence far removed from the articular region. In the amphibia it is modified in precisely the opposite direction; grafting itself more and more completely upon the pre-coracoid border, it comes finally to enter (Cystignathus and Dactylethra[3]) into part formation of the glenoid facet. Sabatier, to whom these facts were known, regards (*op. cit.*) the mammalian coracoid process as identical with the base of the ventralmost coracoid spur of the Lacertilia, and he realises the difficulty of the position, in admitting his inability to find a distinct representative of it in the shoulder-girdle of the monotremes.[4] He further homologises the coracoid process of the mammal with the pre-coracoid (clavicle) of the Amphibia; wherefore his view demands, if the observations of Hoffmann and Mivart be correct,

[1] *Cf.* Flower, *Proc. Zool. Soc.*, 1882; and Parker, *Phil. Trans.*, pt. i., 1885.

[2] *Loc. cit.*, p. 398.

[3] Parker, "Monograph on the Shoulder-Girdle and Sternum," *Ray Soc.*, 1868, pls. vi. and vii.; also Sabatier, *loc. cit.*, pl. 1.

[4] Balfour has asserted this objection still more strongly, *Comp. Embryology*, vol. ii. p. 496.

the demonstration of a direct relationship between the mammalian clavicle and coracoid process, such as is nowhere forthcoming.

The epi-coracoid of the monotreme now demands further consideration. In the young Ornithorhynchus here dealt with, the cartilaginous girdle was subdivided (fig. 5) into coraco-scapular and epi-coracoid plates; segmentation of the glenoidal region had not as yet been effected. Examination of the epi-coracoid (*co'.*) shows that *its dorsal border extends to within the area of the glenoid facet* (it is coincident in position with that of the coracoid process of the rabbit, fig. 2). Shorten up the epi-coracoid as it there stands, and together with it the true coracoid (*co.*), and there would result absolutely the condition of the six-weeks' rabbit.

It is universally conceded that the shoulder-girdle of the monotremes is of a persistently low type, and the remarkable fact that its characters should have remained unchanged in two creatures so diversely modified as the existing Ornithorhynchus and Echidna is in itself a powerful argument in favour of the supposition. Haeckel and Huxley have pointed out[1] that the former animal departs, in all probability, least from the ancestral type. If this be true of its shoulder-girdle, it becomes highly instructive to observe that in it the coracoid region is, as a whole, larger and more expansive than with the Echidna. If, moreover, the girdle of Ornithorhynchus as it exists is representative of the primary term in the mammalian series, that must have been characterised by a coracoid of considerable dimensions, derivative, not of a highly-modified fenestrated type, but of a lowly expanded sheet-like one, no less primitive in its essential characters than is the mammalian vertebral column itself. It must have been a structure for which a parallel most nearly exists to-day in the lower amphibia; and if absorption had taken place, it could only have done so to an insignificant degree.

The coracoid plate of the monotreme would appear then to differ from that of all other vertebrates in being very early segmented into two portions; the anterior of which, in mammals and in them alone, ossifies separately to form the epi-coracoid.[2] While

[1] *Cf.* Huxley "On the Application of the Laws of Evolution," &c., *Proc. Zool. Soc.*, 1880.

[2] The term "epi-coracoid" was first applied here, as stated at the outset, to a distinct element of the mammalian girdle. It has come, in the course of time, to

it is clear that, with respect to this, the mammalian shoulder-girdle is at variance with that of all other animals, it is no less obvious—should the homologies of its parts here formulated prove to be correct—that its characters are constant for the whole mammalian class. Three centres of ossification are set up, such as are met with nowhere else; the epi-coracoid, instead of forming an exceptional element present only in the monotremes, comes to form a distinctive one which can be recognised throughout; the coracoid bar, contrary to that which obtains elsewhere, diminishes in importance and is ultimately suppressed.[1]

The shoulder-girdles of the sloths and ant-eaters are well known to be fenestrated; but the most superficial examination of them shows that the membranous areas present have nothing to do with the fenestræ of the lower animals; they are secondary developments, appearing at the base of the coracoid subsequent to modification along the lines here laid down. Fenestration of the coracoid element, so marked among the lower amniota, is the exception among mammals.

Goette has shown (*loc. cit*) that the cartilaginous predecessor of the mammalian clavicle early unites with its fellow in the middle line; the tract resulting from this coalescence eventually segments into five pieces (fig. 6), viz.:—paired clavicular bars (*cl'.*), two small nodules (*cl'.*), which represent the "lateral episterna" of Gegenbaur ("Omosterna" of Parker, *loc. cit.*), and a median episternum (*cl'.*).

The lateral episterna are stated by him to become attached to the clavicle, or converted into the sterno-clavicular ligament. The middle piece enters into connection with the omosternum,

be extended to the unossified inner border of the primary cartilaginous girdle of the lower air-breathing vertebrates, which is never segmented off. That, as shown by Goette for the frog (*op. cit.*, pl. xxxii. figs. 34–6), is formed by the secondary fusion of the inner ends of the coracoid and pre-coracoid bars; and as such it cannot answer to the mammalian epi-coracoid, which arises as an expansion of the posterior (coracoid) bar alone. The extension of the term is therefore most unfortunate, and productive, as it has been, of a confusion between a definite bony element and a cartilaginous or, at best, superficially calcified *area*, which but roughly corresponds with it.

[1] Martens, in his (the latest) paper "On the Monotreme Girdle," upholds the view that in the higher mammalia the "epicoracoïdien disparaît complétement" (*Ann. Sci. Nat.*, ser. v. vol. xix., 1874). Fletcher's "Catalogue of Papers and Works relating to the Orders Marsupialia and Monotremata" is very welcome (*Proc. Linn. Soc., New South Wales*, vol. ix. pt. iii.).

and either becomes confluent therewith (mole), or undergoes a retrogressive metamorphosis within its perichondrium (Lepus). If, as is so well established, the lateral bars represent the primary predecessors of the clavicles, this median episternum can only represent that of the interclavicle—add it, especially as recorded by Goette in the mole (fig. 6), to the shoulder-girdle of the placental as here interpreted, and the distinction between that and the girdle of the monotreme breaks down.

As regards the monotremes, the only alternative hypothesis which seems to me possible is, that the coracoid bar may have become secondarily expanded, and hence modified in the precisely opposite direction to that of the higher placentalia. Although conceivable, this is for obvious reasons highly improbable. The study of their embryology can alone settle that question, while it must clear up the homology of the episternum; and in view of the exhaustive inquiry into the same now dawning, I have thought it binding to call attention to the facts herein recorded.

In the specimen of Ornithorhynchus here figured the right coracoid sheet underlay the left one. Parker records (*Monograph on the Shoulder-Girdle*) the opposite condition for the specimens which he dissected.

EXPLANATION OF PLATE VIII.

a. Acromion.
cl. Clavicle.
cl'. Inter-clavicle (episternum fig. 6).
cl''. Lateral episterna.
co. Coracoid.
co'. Epicoracoid (coracoid process, figs. 1–3).
gl. Glenoid facet.
s. Scapula.
s'. Supra-scapula.
st. Sternum.
st'. First sterebra of adult.
st''. Omosternum.

Fig. 1. The shoulder-girdle of a young rabbit, at three weeks of extra-uterine life, exclusive of the clavicle; natural size.

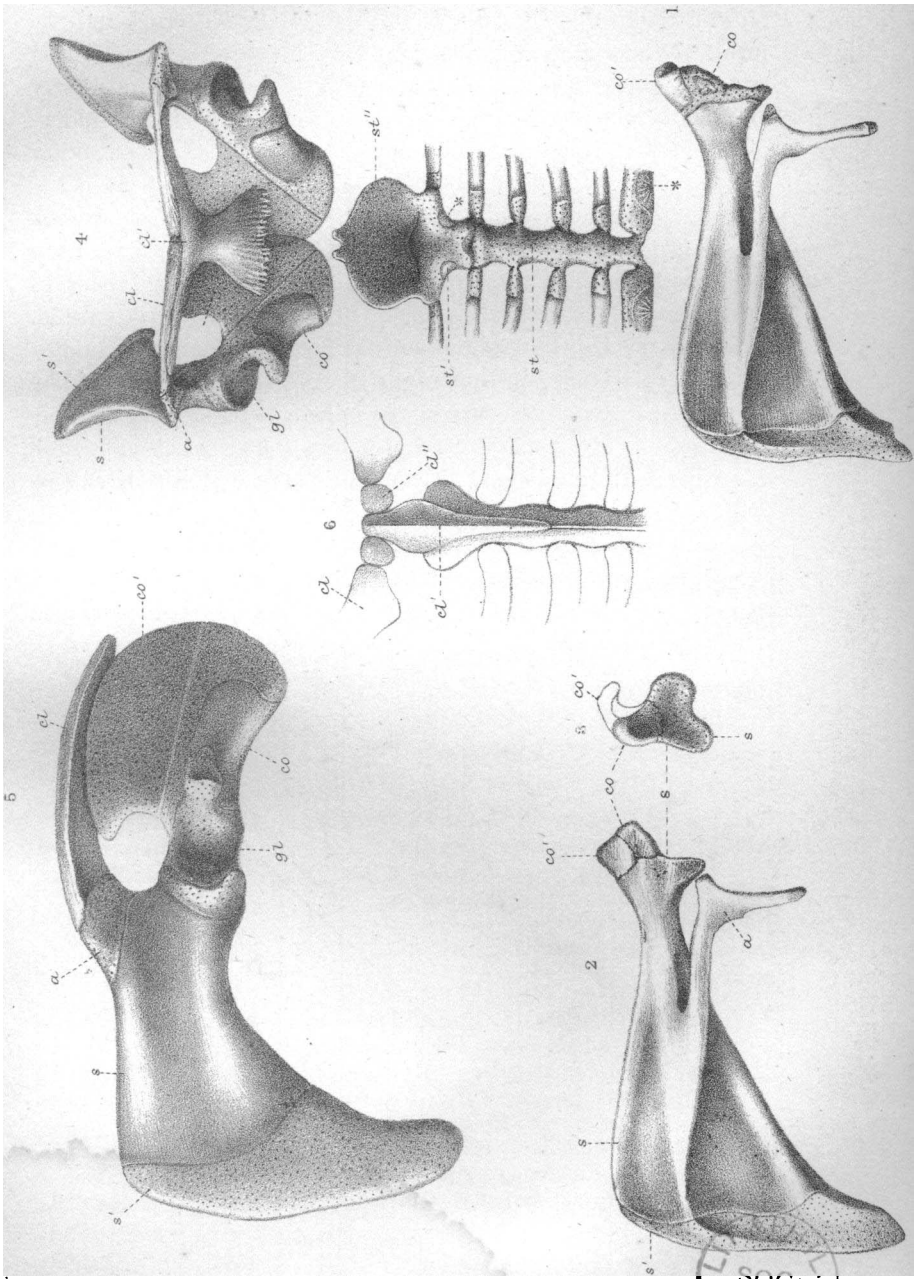
Fig. 2. A similar girdle, three to four weeks later; natural size.

Fig. 3. The glenoid facet of the same; natural size.

Fig. 4. The entire shouder-girdle and sternal apparatus of a young Ornithorhynchus; front view. The omosternum has been released from its connection with the inter-clavicle; × $2\frac{1}{2}$.

Fig. 5. The right half of the same, after removal of the inter-clavicle. Drawn to the same scale as fig. 2 for sake of comparison.

Fig. 6. The segmenting sterno-clavicular apparatus of a young mole. After Goette.



G.B.H. & G.M. Woodward del
G.M.W. lith.

Mammalian Coracoid.

Hen. Newman & Co. imp.