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THE DEVELOPMENT OF TARSUS IN GALLUS DOMESTICUS

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As generally known in birds the hock joint, *articulatio tarsi*, is a simple *ginglymus* in contrast to conditions in other tetrapoda where two rows of tarsal bones take part in the formation of this joint.

The development of the tarsal joint in birds has been studied in various species, *e. g.* in *Larus*, *Anser*, *Anas*, *Struthio*, etc., but strange to say, it has never been thoroughly investigated in *Gallus domesticus*. In the literature on the embryology of *Gallus domesticus* this lack of knowledge is even particularly emphasized *e. g.* by *Frank R. Lillie* who in "The development of the chick" (page 545) describes how at least three tarsal cartilages are present in the embryo and who continues: "The actual make up of these elements is as yet poorly known . . ."; in "The avian embryo" (page 1013) *Alexis L. Romanoff* states: "The embryonic elements of the avian foot are somewhat obscure".

PREVIOUS STUDIES

Among the previous studies on the nature of the development of the tarsus in *Gallus domesticus* the ones from 1863 and 1864 by *C. Gegenbaur* should be mentioned. This author was the first to demonstrate in chick embryos anlagen of tarsal bones which later in the embryonic development fuse with the tibia and the metatarsal bones. In 6-day-old chick embryos *Gegenbaur* found an undifferentiated tissue mass between the cartilaginous *ossa cruris* and *ossa metatarsalia*; five to six days later this tissue mass has been differentiated into two cartilaginous elements *viz.* one proximal or *crural*, and one distal or *metatarsal*; the

crural element will later fuse with the tibial bone, the metatarsal element with the metatarsals II—IV. To quote *Gegenbaur* this coalescence is “nicht etwa bloss eine feste Aneinanderfügung mittels eines heterogenen Gewebes, sondern eine kontinuierliche Verschmelzung der Grundsubstanz der beiderseitigen Knorpel”. Although the original outlines become imperceptible after the coalescence *Gegenbaur* was of the opinion that the crural as well as the metatarsal elements maintain a certain independence because the ossification of the latter occurs quite independently of the ossification of the bones with which they have fused. The author points out how the intertarsal articulation becomes the site of motion as opposed to conditions in mammals in which motion occurs in the crurotarsal joint.

Conversely, *G. Baur* 1883 and *Alice Johnson* 1883 demonstrated on the 7th day of embryonic life three tarsal anlagen, *viz.* two proximal and one distal. At a later stage the two proximal anlagen coalesce and unite with the tibial bone and the distal anlage unites with the metatarsal bones. Both of the latter authors describe an upward process from the proximal anlage, “the ascending process of the astragalus”, reaching up to the dorsal surface of the tibia and coalescing with the latter before hatching.

Among the studies from recent years should be mentioned works by *Siegelbauer*, *Lutz*, and *Holmgren* whose findings seem to make it possible to clarify which ones of the tarsal elements are incorporated in the crural and the metatarsal elements.

OWN INVESTIGATIONS

Material and technique.

For the present investigation I have used pelvic limbs from chick embryos 6, 7, 8, 9, 10, 11, 13, and 17 days old together with pelvic limbs from one-day-old chicks. The embryos were fixed in Bouin's fixing fluid or in formalin, stained in toto using haemalum or Hansen's chromalumdioxyhaematein, embedded in paraffin, and cut into serial sections. Wax plate reconstructions according to Born's method were made of the tarsus of 7 and 8 days old embryos at 50 × magnification.

Descriptions and findings.

Embryo. 6 days old.

As will be seen from Fig. 1 the cartilaginous anlagen of tibia, fibula, and metatarsals II, III and IV are clearly visible on the

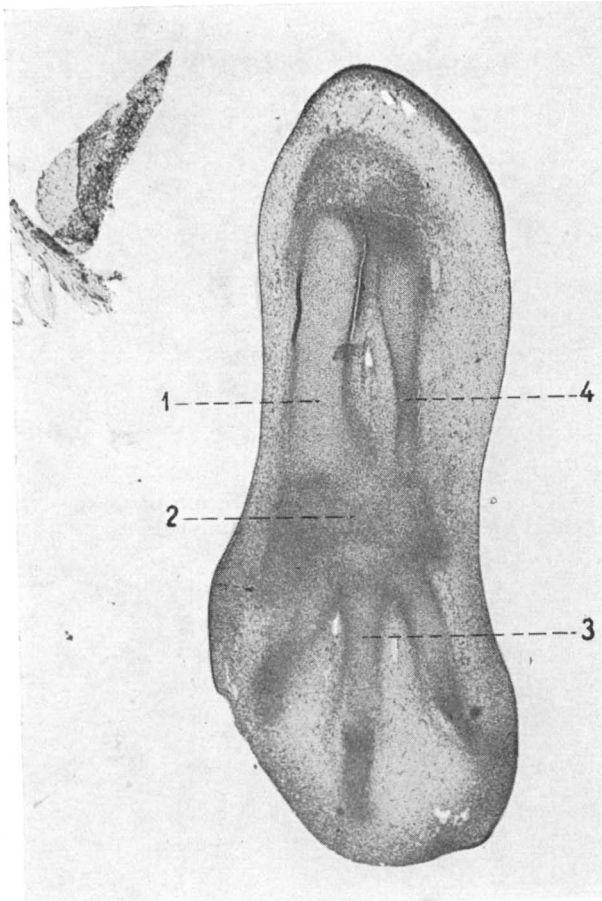


Fig. 1. Embryo, 6 days, frontal-section of pelvic limb, 27 \times .
1. tibia, 2. zone of precartilaginous tissue, 3. ossa metatarsalia, 4. fibula.

6th day of embryonic life. The fibula is highly developed being of the same length as the tibia. Between the crural and the metatarsal bones a wide zone of precartilage can be seen. The differentiation to cartilage is just setting in, manifesting itself as paler areas but any distinct primordia to tarsal bones cannot be discerned.

Embryo. 7 days old.

In the frontal section presented in Fig. 2 a well-defined cartilaginous anlage of the bones is seen. Fibula has not grown to the same extent as tibia and does not reach the distal end of the

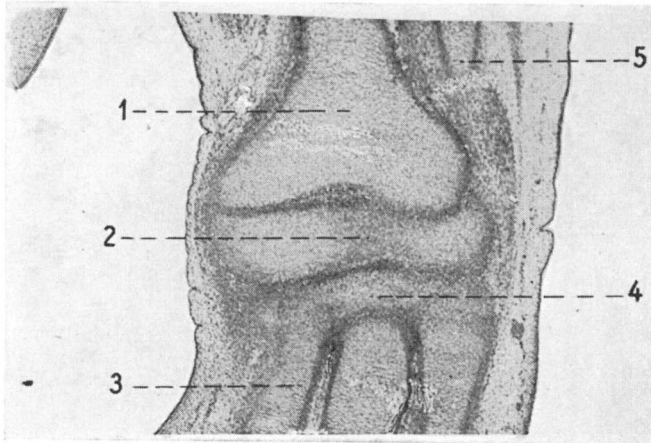


Fig. 2. Embryo, 7 days, frontal-section of tarsus, 37 \times .
1. tibia, 2. crural element, 3. os metatarsale II, 4. metatarsal element,
5. fibula.

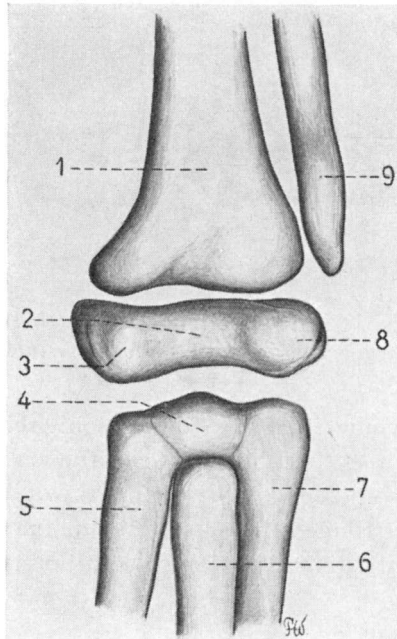


Fig. 3. Embryo, 7 days, reconstruction model of tarsus, 32 \times .
1. tibia, 2. crural element, 3. anlage of the medial condyle, 4. metatarsal
element, 5. os metatarsale II, 6. os metatarsale III, 7. os metatarsale IV,
8. anlage of the lateral condyle, 9. fibula.

latter. Also an anlage of os metatarsale I is present at this stage. In the original mass of precartilage between the crural and the metatarsal bones two cartilaginous elements have developed now, *viz.* one proximal element arranged below tibia and fibula, in the terminology of *Gegenbaur*: the crural element of the tarsus, and one distal element arranged above the metatarsal bones, *viz.* the metatarsal element.

In the reconstruction model, Fig. 3, the crural element is seen to be well-defined, being of an almost quadrangular shape, medially a little higher than laterally where it encloses the distal end of the tibia. The medial half of the proximal surface is rather flat whereas the lateral part has a concave facet for tibia. Centrally on the distal surface a concavity corresponds to a small projection from the proximal surface of the metatarsal element. On the dorsal surface of the crural element two hemispherical prominences are demonstrable, *viz.* anlagen of the condyles, cf. Fig. 3, 3.

The metatarsal element, Figs. 2 and 3, is inserted as a wedge

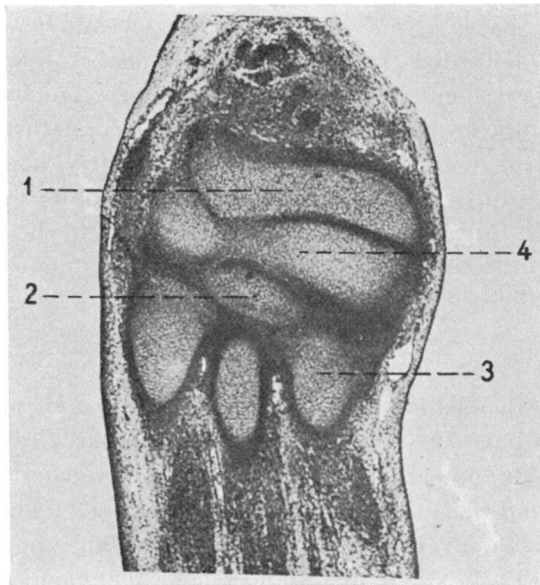


Fig. 4. Embryo, 7 days, frontal-section of tarsus, 37 \times .
1. distal part of tibia, 2. metatarsal element, 3. os metatarsale II,
4. crural element.

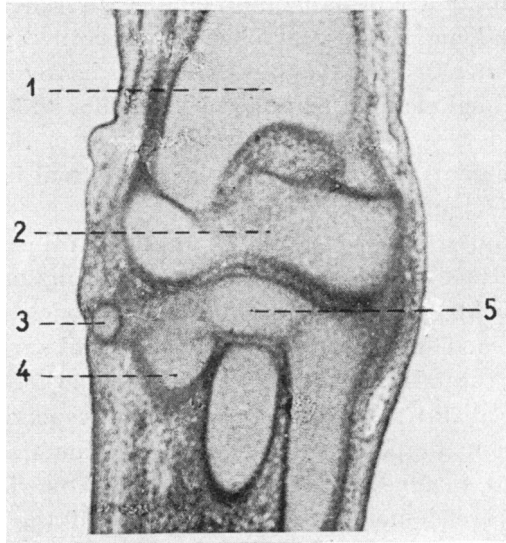


Fig. 5. Embryo, 8 days, frontal-section of tarsus, 40 \times .
 1. tibia, 2. crural element, 3. os metatarsale V, 4. os metatarsale IV,
 5. metatarsal element.

between the bases of the anlagen of the metatarsals II and IV, indistinctly delimited from the latter by darker lines. Whereas the metatarsal bone III and the metatarsal element are well-defined it may be rather difficult to decide whether the latter joins the bases of the metatarsals II and IV. It is apparent from Fig. 4, presenting a section stained by chromalumdioxyhaematein, however, that this element has no connection with the metatarsals II and IV; thus there will be an isolated metatarsal element in addition to the crural one.

Embryo. 8 days old.

On the 8th day of embryonic life, Figs. 5 and 6, the tarsal components have further developed. As compared with findings from the 7-day-old embryo the anlage of the two condyles is more prominent and the so-called "ascending process" from the lateral condyl is demonstrable, cf. Fig. 7. Moreover the sagittal section presented in Fig. 7 shows also that the crural element is beginning to coalesce with the plantar surface of the tibia; Figs. 8 shows that the same applies to the metatarsal element and the metatarsal bone III. At this stage demarcation between the metatarsal

element and the metatarsals II and IV has almost disappeared. The fibula has become comparatively shorter.

Later stages of embryonic life

A study on the later embryonic stages shows the further, gradual disappearance of the demarcation lines between the tarsal elements and tibia and metatarsus. In 13-day-old embryos, cf. Fig. 9, coalescence is completed; the tibial and metatarsal diaphyses have started to ossify. The marked vascular ingrowth suggests the later epiphyseal lines, cf. Figs. 9, 2, and 5. These lines and the lines of coalescence do not correspond; hence the conclusion may be drawn that ossification occurs without any

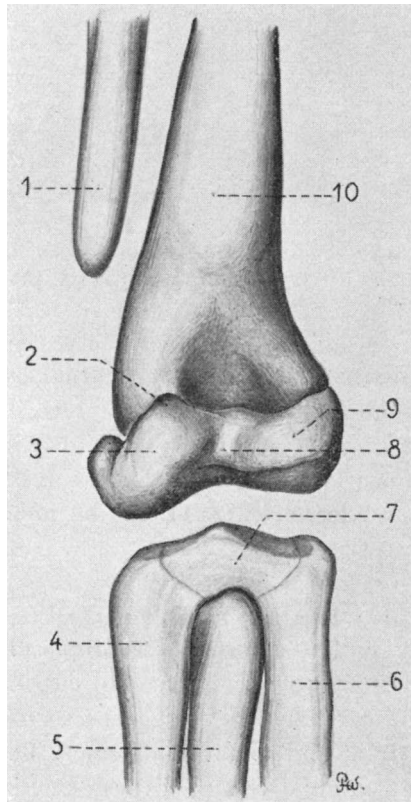


Fig. 6. Embryo, 8 days, reconstructionmodel of tarsus, 29 \times .
 1. fibula, 2. processus ascendens, 3. anlage of the lateral condyle, 4. os metatarsale IV, 5. os metatarsale III, 6. os metatarsale II, 7. metatarsal element, 8. crural element, 9. anlage to the medial condyle, 10. tibia.

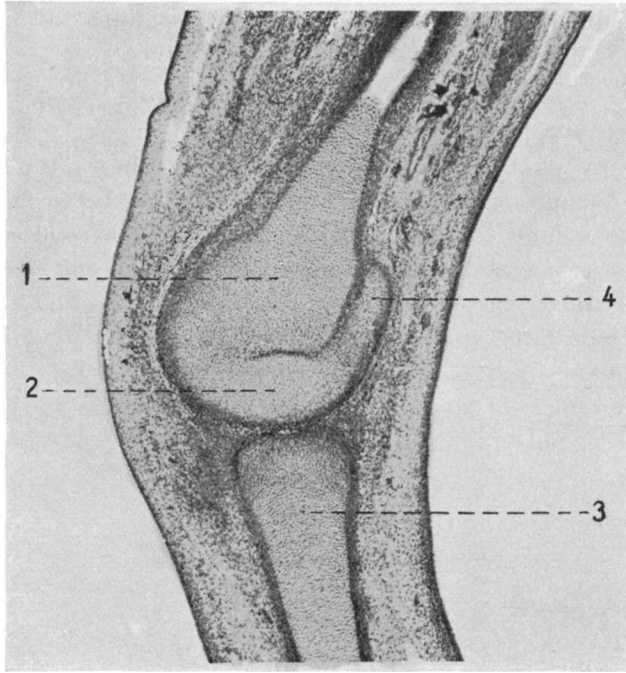


Fig. 7. Embryo, 8 days, sagittal-section of tarsus, 40 \times .
1. tibia, 2. crural element, 3. os metatarsale IV, 4. processus ascendens.

relation at all to the original anlagen. "The ascending process" later to coalesce with tibia has its individual ossification center demonstrable in embryos already on the 17th day of embryonic life, cf. Fig. 10. Examination of one-day-old chicks disclosed the presence of two ossification centers in the tibial epiphysis, one on each of the condyles, cf. Fig. 11. In the metatarsal epiphysis one center only is present, cf. Fig. 12.

COMPARATIVE ANATOMY

In conformity with *Gegenbaur's* findings the present study shows that tarsus is developed from two cartilaginous elements which even at the cartilaginous stage are seen to coalesce completely with the tibial and metatarsal bones. The study failed to provide evidence of a subdivision of these cartilaginous elements into smaller elements corresponding to the individual tarsal components, neither at the cartilaginous nor at the precartilaginous stage. The number of tarsal components involved in these elements can be deduced only on the basis of comparative studies.

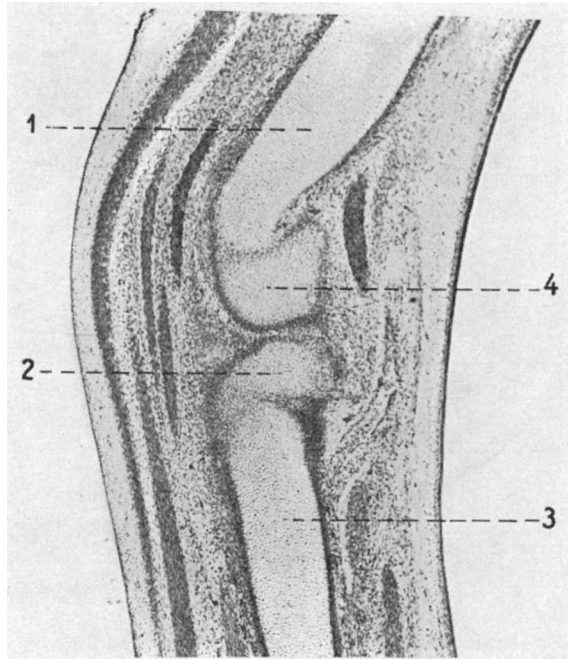


Fig. 8. Embryo, 8 days, sagittal-section of tarsus, 40 \times .
 1. tibia, 2. metatarsal element, 3. os metatarsale III, 4. crural element.

On the basis of such comparative studies *Gegenbaur* arrived at the conclusion that the crural element might be corresponding to tibiale, intermedium, centrale, and fibulare, and also that four tarsal bones formed constituent parts of the metatarsal element. *Gegenbaur's* conclusions were based upon studies on Amphibia and Reptilia in which classes bones are known to coalesce. In Urodela the proximal row includes three cartilages, *viz.* tibiale, intermedium, and fibulare; a centrale is inserted between the proximal and the distal row of tarsal bones. This is not the case in Anura in which two bones are present in the proximal row, astragalus, (formed by coalescence of tibiale and intermedium) and fibulare. *Gegenbaur* found good reason to assume that the apparently missing centrale had been included in the astragalus which thus did not remain a true astragalus. Studies on Chelonia made *Gegenbaur* realize that tibiale and intermedium had coalesced and in addition had joined with centrale and fibulare. The four elements which in Urodela are separate have in Chelo-

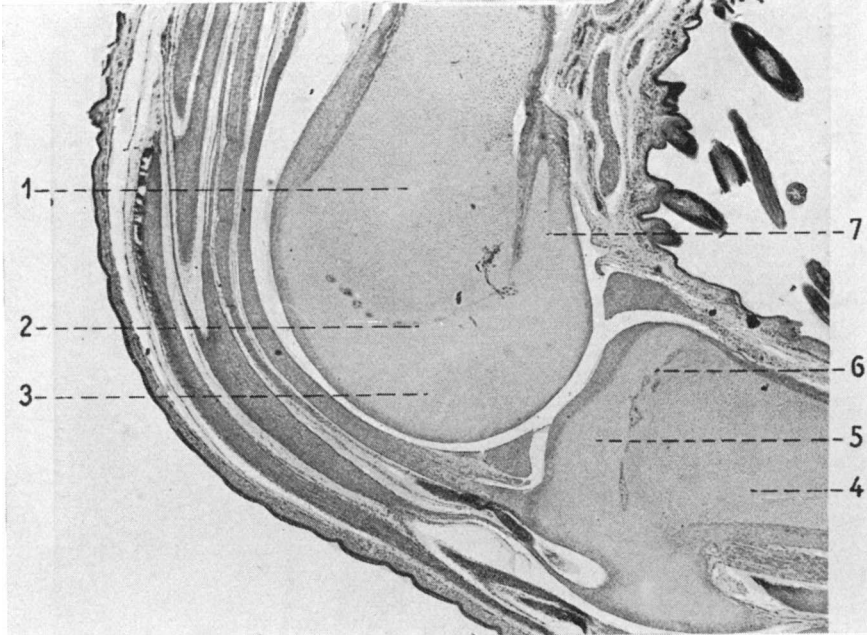


Fig. 9. Embryo, 13 days, sagittal-section of tarsus, 24 \times .
1. tibia, 2. vascular line, 3. crural element, 4. os metatarsale IV, 5. metatarsal element, 6. vascular line, 7. processus ascendens.

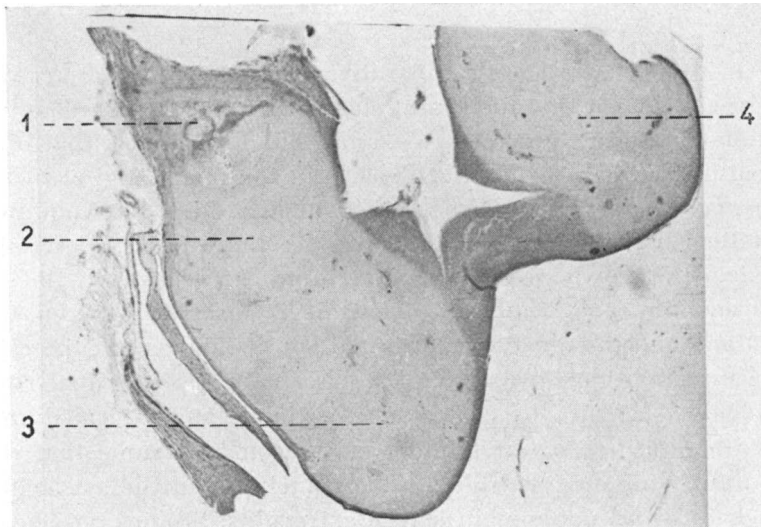


Fig. 10. Embryo, 17 days, frontal-section through the condyles, 23 \times .
1. ossification-center of processus ascendens, 2. processus ascendens,
3. lateral condyle, 4. medial condyle.

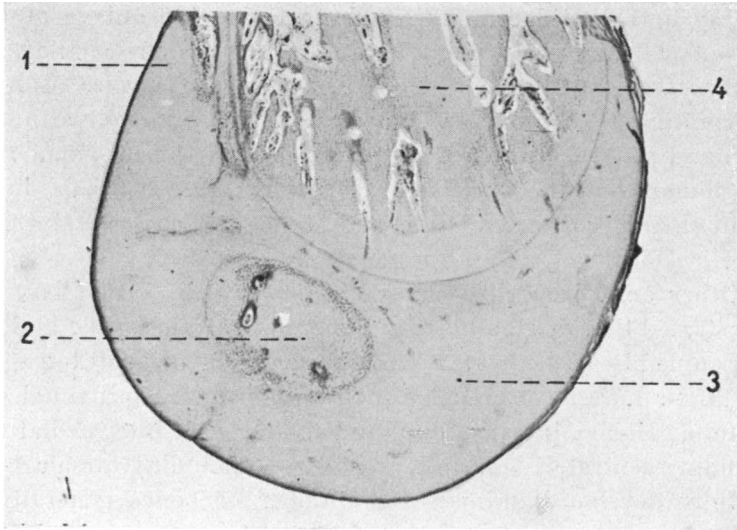


Fig. 11. One-day-old chicken, sagittal-section of tibia, 18 \times .
1. processus ascendens, 2. ossification-center, 3. epiphyse, 4. diaphyse.

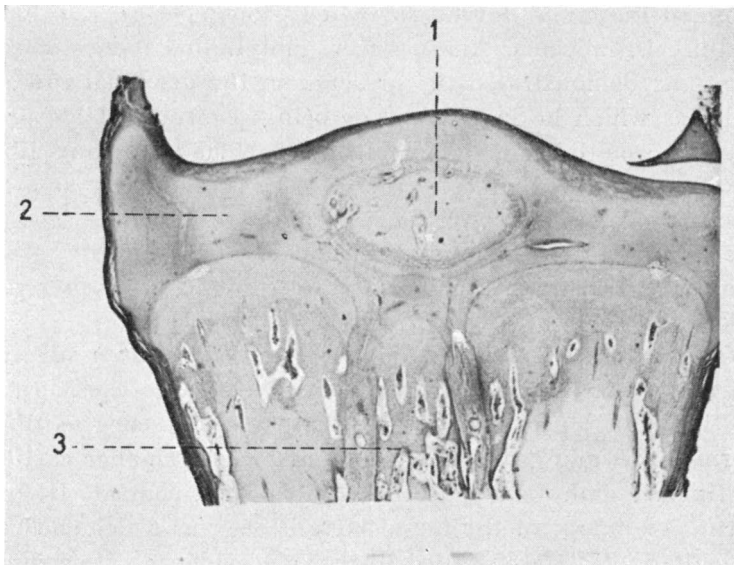


Fig. 12. One-day-old chicken, frontal-section of metatarsus, 18 \times .
1. ossification-center, 2. epiphyse, 3. diaphyse.

nia coalesced into one bone. The feature represents the normal finding in Lacertidae and *Gegenbaur* found the anlage of this particular bone to be present in the form of a single cartilage.

Siegelbauer 1910 studied conditions in the species of *Anas* interpreting his findings in accordance with *Gegenbaur* although he found a development of two cartilages in the proximal row, the fibulare and the "tritibiale", viz. the coalesced tibiale, intermedium, and centrale. Fibulare and "tritibiale" coalesce at a later stage.

Other embryological studies (*Schmalhausen* 1910) have demonstrated that originally the number of centrales was 4 and not as assumed by *Gegenbaur* 1 or 2. Hence, in the original tetrapoda the tarsus may have included 3 rows of bones: a proximal row including tibiale, intermedium, and fibulare; an intermedial row including centrale 1—4; and a distal row including tarsale 1—5. In fully developed animals the number of bones generally is reduced because of coalescences, but ontogenetic studies have demonstrated the presence in foetal life of anlages of the original tarsal components.

Such studies on avian species have been carried out by *Lutz* in 1942 and *Holmgren* in 1933 and 1955; both of these authors examined the tarsal development in various species, e. g. *Larus*, *Struthio*, *Dromiceius*, *Anas*, *Anser*, and *Gallus domesticus*. In *Anas* *Lutz* demonstrated the presence in the proximal row of 3 cartilages which he interpreted as being: centrale tibiale proximale, centrale tibiale distale, and fibulare. The pre-hallux, tibiale as well as intermedium, was found to be present only as a condensation of mesenchyme; the remaining two centrales, viz. centrale fibulare proximale and distale were assumedly absent. Anlages of 5 distinct, tarsal bones were found to be present in the distal row.

On the basis of studies on avian species *Holmgren* suggested that the proximal row might include (1) a large cartilage, viz. the "tritibiale", probably developed by a coalescence of tibiale, intermedium, and centrale I and II, and (2) a smaller cartilage, viz. fibulare and, distally to this, centrale IV; centrale III being absent. An Anlage of the tarsal bone is seen as a detached disk of cartilage. *Holmgren* failed to provide evidence of a presence of tibiale.

On the basis of the investigations cited it should be noted that highly deviating opinions still exist both as regards the

terminology and the homology of the avian, embryonic, tarsal components. *Holmgren* emphasizes the importance of continued, comparative investigations of the topic with a view to obtaining a more reliable interpretation.

ACKNOWLEDGEMENT

I want to express my gratitude to the principal of the Laboratory for Fowl Investigation, Assistant Professor *H. Marthedal*, D. V. M., who placed the necessary material at my disposal. The reconstruction model was drawn by Mr. *Poul H. Winther*, Illustrationist; the micrographies were prepared by Assistant Professor *Anker Hansen*. I am much obliged for all the assistance I have received.

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SUMMARY

The author has investigated the development of tarsus in *Gallus domesticus* using embryos of various ages together with one-day-old chicks. The author found that the anlage of tarsus is present as two cartilages, one proximal *viz.* the so-called crural element, and one distal: the metatarsal element. Even at the cartilaginous stage these elements are seen to coalesce with the tibia and the metatarsus, respectively. In 13-day-old embryos the coalescence is completed and at the same time the primary signs of incipient ossification are noted, ossification being independent of the anlage of the tarsal components demonstrable very early in the embryonic life. The comparative anatomy, *viz.* which ones of the tarsal components may be involved, is discussed.

ZUSAMMENFASSUNG

Die Entwicklung des Tarsus bei Gallus domesticus.

Verf. hat die Entwicklung des Tarsus bei Embryonen verschiedenen Alters sowie Eintagskücken von *Gallus domesticus* untersucht und findet, dass der Tarsus in zwei Knorpelstücke, ein proximales, das sogenannte crurale Stück und ein distales, das metatarsale Stück, angelegt wird. Schon im knorpeligen Stadium wachsen diese Stücke teils mit der Tibia, teils mit dem Metatarsus zusammen. Diese Zusammenwachsung ist vollständig bei Embryonen von 13 Tagen; gleichzeitig tritt die Ossifikation ein, die sich unabhängig von den in den früheren Embryonalstadien angelegten Tarsalkomponenten vollzieht. Die komparative Anatomie, d. h. welche Tarsalkomponente die erwähnten Knorpelstücke enthalten, wird diskutiert.

RESUMÉ

Udviklingen af tarsus hos Gallus domesticus.

Forf. har undersøgt udviklingen af tarsus hos *Gallus domesticus* på fostre af forskellige alderstrin samt på daggamle kyllinger. Forf. har fundet, at tarsus anlægges som to bruskstykker, et proximalt, det såkaldte crurale stykke, og et distalt, det metatarsale stykke. Endnu i det bruskede stadium vokser disse stykker sammen dels med tibia, dels med metatarsus. Denne sammenvoksning er komplet hos fostre på 13 dage; samtidig optræder de første tegn på begyndende forbening, der foregår uafhængigt af de i de tidligere fosterstadier anlagte tarsalkomponenter. Den komparative anatomi, det vil sige hvilke tarsalkomponenter, der indgår i de ovenfor nævnte bruskstykker, diskuteres.

(Received July 9. 1962).