EUDIARTHRODIAL JOINTS IN FISHES

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INTRODUCTION

The work of Bernays (1878), Sémon (1899) and Lubosch (1910, 1938) has led to the classification of the several types of joint in a morphological series. From the simplest to the most complex forms these are: (1) synarthroses, in which the skeletal parts are attached to one another by cartilage, fibro-cartilage, fibro-tendinous or connective tissue (Fig. 3); (2) schizarthroses, in which a number of separate cavities appear in these tissues; (3) hemidiarthroses or periarthroses, in which there is a single joint cavity occupying the centre of the joint while the articulating elements are still united round the periphery; and (4) eudiarthroses, in which the articulating elements are separate, the joint cavity being limited peripherally by synovial tissues (Fig. 1). The authors quoted are also agreed that these morphological forms represent a true evolutionary series, suggesting that the typical Selachii, Dipnoi, Chondrostei and Holostei, which are said to possess only the first three of the above types, are primitive in this respect. On the other hand, those groups of animals to which the possession of eudiarthroses is said to be confined, the Raioidei, Teleostei and Tetrapoda, are considered to have acquired these structures as a new evolutionary advance which has been made independently in each group.

Lubosch (1910, 1938) considers that in urodele Amphibia the eudiarthroses found in the shoulder, elbow and hip, with their synovial structures and capsules, are new formations, and that it is doubtful whether those forms which do not now possess them, such as *Proteus*, ever did possess them. Schwarz (1935), on the other hand, from a detailed study of the wrist joint in several urodeles, has decided that the forms which have a well-developed joint cavity of hemidiarthrodial type, such as *Salamandra*, are the more primitive, while those, such as *Necturus* and *Amphiuma*, in which the cavity is small, are secondarily degenerate in this respect. Lubosch regarded this interpretation as doubtful, but in a recent study of the knee joint (Haines, 1942*a*) a similar conclusion to that of Schwarz was reached. This study provided evidence that in primitive tetrapods, including the ancestors of the urodeles, there was a fully developed eudiarthrodial joint with menisci and cruciate ligaments, but that these have been partially or wholly lost in modern forms. On the other hand, as already noted, it has been generally agreed that eudiarthroses are not found in the more primitive types of fishes, and are new developments in tetrapods.

Yet in the figures illustrating a study of the microscopic structure of the jaws of fishes (Haines, 1937) there are depicted, incidentally to the main theme, what are obviously fully developed eudiarthrodial joints, similar in every essential to those of tetrapods, and this in a series including the primitive types *Polypterus*, a direct descendant of the early palaeoniscids (Romer, 1933), and *Protopterus*, one of the surviving lungfish, as well as several Teleostei. It has needed only the addition of the two surviving holosteans, *Lepidosteus* and *Amia*, both fortunately available from the Zoological Society's collection, to complete a series indicating that the eudiarthrodial condition is primitive in the jaw joint for all bony fishes. These specimens will be described and figured here, and the bearing of the conclusions reached on the phylogenetic development of joints may then be discussed.

OBSERVATIONS

Lepidosteus osseus. In the jaw joint (Figs. 1, 2) the quadrate (*Quad.*) is well ossified, and carries a convexity formed of a layer of calcified cartilage (*cal.ct.*) overlaid by a layer of hyaline cartilage (*hyl.ct.*). The cells of the calcified cartilage are hypertrophied,

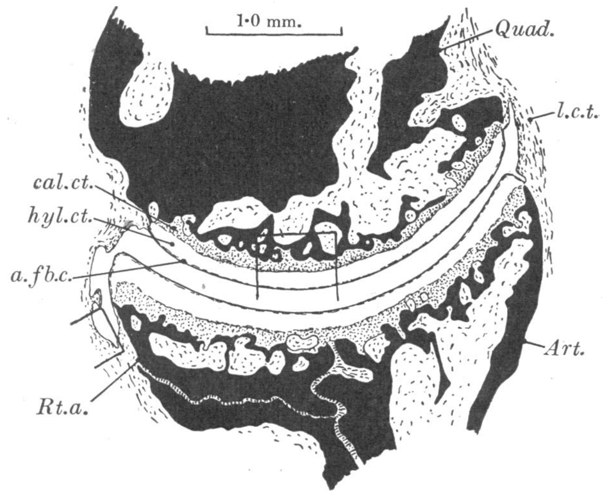

Fig. 1. The jaw joint of *Lepidosteus osseus*, to show a fully developed eudiarthrodial joint in a primitive type of bony fish.

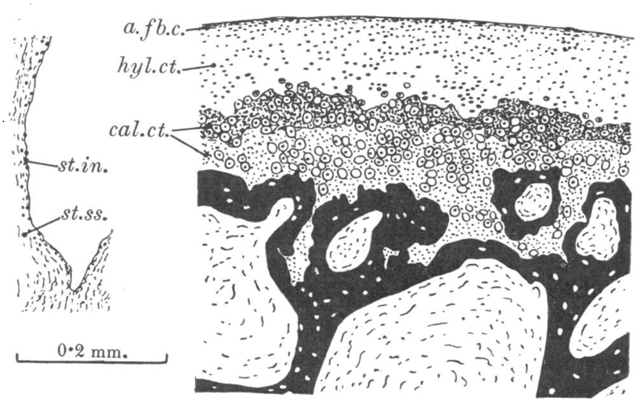

Fig. 2. Enlargements of the parts marked off in Fig. 1, showing a part of the synovial membrane and a part of the articular cartilage of the quadrate bone.

while those of the hyaline cartilage are smaller and rounded. Near the articular surface the cells are flattened and the matrix shows a thin acidophilic fibro-cartilaginous layer (*a.fb.c.*) underlying the surface itself. The mandibular articular surface is supported by two bones, the articular (*Art.*) and retro-articular (*Rt.a.*) which ossify in Meckel's cartilage, whose structure resembles that of the quadrate cartilage. Peripherally the joint is surrounded by loose connective tissue (*l.c.t.*), and inside this is a fully differentiated synovial membrane, with the two layers of classical description (Lubosch, 1938), a stratum intimale (*st.in.*) and a stratum subsynoviale (*st.ss.*). The tissue is not sufficiently well preserved for more detailed description, but its general arrangement, and that of the whole joint, resemble closely those of a tetrapod (cp. Fig. 6), and indeed can hardly be distinguished without a close examination of the osteocytes.

The joint between the epi- and pharyngo-branchial elements of the third (first true) branchial arch (Fig. 3) is of the simplest possible construction, a relatively thin layer of fibro-cartilage (*fb.ct.*) uniting the cartilaginous epiphyses of the two bones to form a simple synarthrosis. Peripherally this layer passes gradually into the connective tissue of the perichondrium (*p.c.t.*).

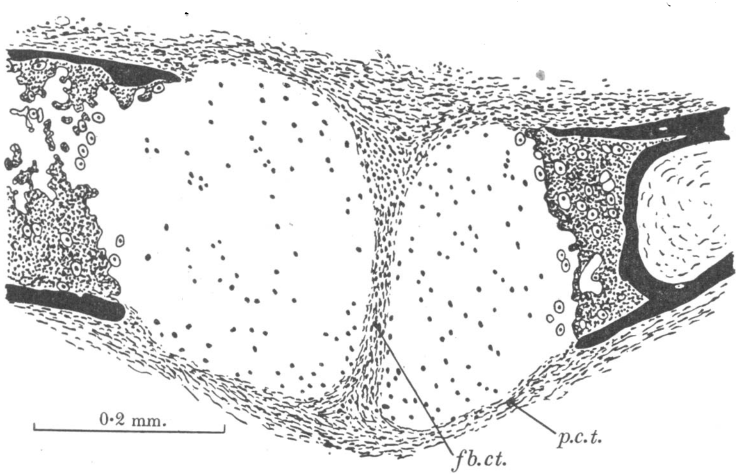

Fig. 3. The pharyngo-epibranchial joint of the third branchial arch of *Lepidosteus osseus*, to show a very simple type of joint co-existing with the complex type shown in Fig. 1.

In the fins the joints (figured by Lubosch, 1910, Fig. 34) are hemidiarthroses. The joint surfaces are not so smooth as in the jaw joint, but the cavity is well developed, though the bones are still joined at their periphery by a ring of cartilaginous and fibro-cartilaginous tissue.

Amia calva. This is a rather advanced holostean type, so that it is less likely to illustrate primitive conditions than *Lepidosteus*. The jaw joint is again eudiarthrodial, but the hyaline cartilage is covered with a thick layer of articular fibro-cartilage. The branchial joints, of much greater absolute size than in *Lepidosteus*, may show small joint cavities in the articular tissue (which is a mass of fibro-cartilage containing areas of hyaline cartilage), and the joints must therefore be regarded as poorly developed schizarthroses.

In the pectoral fin Lubosch (1910) has figured a hemidiarthrodial condition at the articulation of the proximal radial with the girdle and with the basal cartilage. In my specimen there is a well-defined joint cavity with occasional strands of connective tissue projecting into it from the articular surfaces. Peripherally there is a synovial membrane with its two strata, so that the joint has reached a eudiarthrodial condition.

Joints of bony fishes. In the primitive fishes already described examples have been found of all the main types of joints met with in vertebrates, and this is also known to be the case in other bony fishes. The development of a wide range of varieties of joint must therefore be regarded as normal in these forms. In the dipnoan *Protopterus* (Haines, 1937) the jaw joint is a eudiarthrosis, though the quadrate and Meckel's cartilage remain entirely hyaline throughout life, for they are never calcified or replaced by endochondral bone or marrow. These peculiarities are, however, secondary, for, as Watson & Gill (1923) have shown, in the more primitive dipnoans of Devonian times there was a well-developed articular bone supporting the articular cartilage. Thus in these early forms the resemblance to the type of joint found in *Lepidosteus* must have been very close. In the joints of the fins of bony fishes Klaatsch (1896) and Lubosch (1910, 1938) have found hemidiarthroses, schizarthroses and synarthroses, the more highly developed condition being usually present in the larger joints, and the less highly developed in the smaller joints—particularly in the distal parts of the fins. The actual tissues that form the synarthroses differ in the three existing genera, being tendinous, fibro-cartilaginous or fibrous.

Again, in *Polypterus* the jaw joint (Haines, 1937) is a typical eudiarthrosis, with Meckel's cartilage ossified to form a well-developed articular bone, and with a hyaline articular cartilage covered with a thin layer of articular fibro-cartilage. In the early palaeoniscids *Elonicthys* (Watson, 1925) and *Nepatoptychius* (Watson, 1928) and the Devonian crossopterygian *Sauripterus* (Broom, 1913) the articular was well developed and carried a definite surface for the cartilage of the joint, so that here again there is every reason to believe that a eudiarthrosis was developed. In other parts of the body less highly developed joints have been described in the fins of *Polypterus* and *Calamoichthys* by Lubosch (1910), and my own sections from the branchial region of *Polypterus* show a structure similar to that in *Lepidosteus*.

Thus all these primitive types of bony fish agree in the possession in different parts of their bodies of joints of various types, but always with the most highly developed type in the jaw joint, and the least highly developed in the smaller joints of the branchial region and the distal parts of the fins.

In Teleostei (Lubosch, 1910, 1938) the various types of joint are well known as regards their general structure, and they are similar to those of more primitive fishes. However, a detailed study of a teleostean synovial joint by modern histological methods might well be of the greatest interest.

Elasmobranchs and sturgeons. In *Acipenser*, the only genus of sturgeons whose joints have been studied, Lubosch (1910) observed in one joint of the pectoral fin a small cleft, but otherwise he found only synarthroses. My own sections from the branchial region confirm these observations; on the other hand, the jaw joint is a schizarthrosis with several small joint cavities lying in a mass of connective tissue (Fig. 4). There can be little doubt, however, that such a structure in the jaw joint is secondarily derived from a eudiarthrodial condition, for, as Watson (1925) and others have shown, the modern Acipenseroidei have lost much of the bony structure of their palaeoniscid ancestors, and the jaws have been reduced to a weak protrusible apparatus.

The Elasmobranchii are more difficult to understand. In the fins of most Selachii, described fully by Bernays (1878) and Lubosch (1910, 1938) as showing what they took to be relatively primitive conditions, there are found only synarthroses (all joints of *Carcharias*), schizarthroses and hemidiarthroses. In *Scyllium* and *Acanthias* the jaw joint is a hemidiarthrosis, while in *Zygaena* and in the holocephalian *Chimaera* (Fig. 5) it makes a closer approach to the eudiarthrodial state, with a synovial membrane

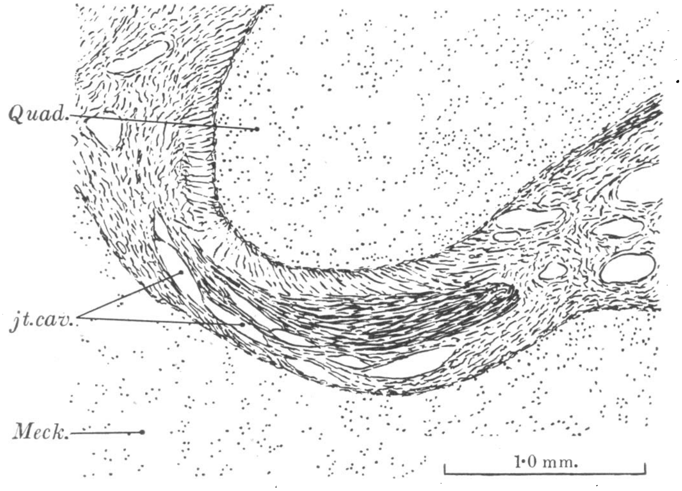

Fig. 4. Jaw joint of *Acipenser ruthenus*, to show a schizarthrosis associated with its predominantly cartilaginous structure, instead of the more usual eudiarthrosis.

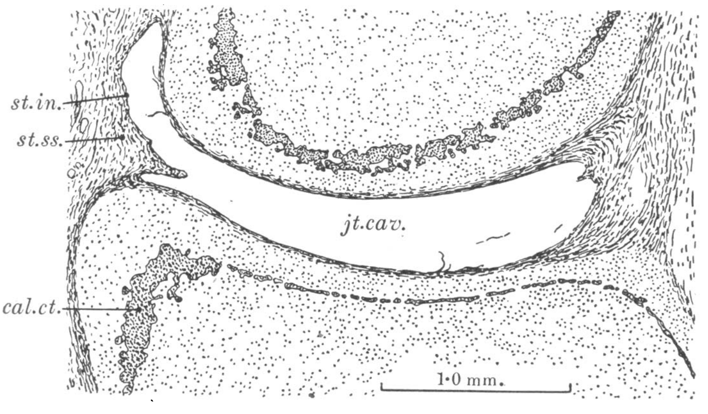

Fig. 5. Jaw joint of *Chimaera monstrosa*, to show an approach to the eudiarthrodial type of joint in an elasmobranch.

(*st.in.* and *st.ss.*) bounding the joint on one side. This partial development of a synovial covering is known also in urodeles (Lubosch, 1910), where it appears to be the result of a secondary simplification of a previously more highly developed type of joint. In the Raioidei, on the other hand, Lubosch (1910, 1938) has found well-developed eudiarthroses.

Whether the elasmobranchs as a whole ever had eudiarthrodial joints is uncertain.

They may have lost them, as have the modern sturgeons, for, though their ancestral history is unknown, there is good reason to believe that they are derived from forms with a more extensively ossified skeleton than they now have (Moy-Thomas, 1939).

Joints of tetrapods. In tetrapods the jaw joint has lost its position as the most highly developed joint in the body, though even in mammals it still maintains its identity as the malleolo-incudal joint. Apart from some of the more distal joints of the anurans, and most of the joints of the urodele amphibians, all the joints of the limbs are eudiarthrodial, and Fig. 6 illustrates the usual, and what is here believed to be the primitive, condition in tetrapods in general. The hyaline cartilage of the epiphysis is covered by a thin layer of articular fibro-cartilage (*a.fb.c.*), thickened in some parts of the joint to form a labrum (*lab.*). Wherever the joint cavity abuts on loose connective tissue there is a well-developed synovial membrane with the usual two layers (*st.in.* and *st.ss.*). The

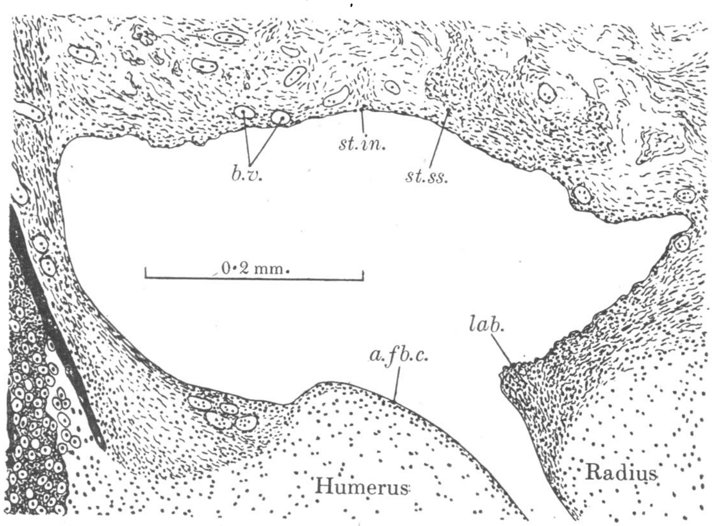

Fig. 6. Part of the elbow joint of *Emys orbicularis*, to illustrate what is here believed to be the primitive type of joint in the limbs of tetrapods, showing the synovial membrane with its stratum intimale and stratum subsynoviale, and the absence of any definite joint capsule.

subsynovial stratum is very vascular (*b.v.*), and blends without interruption with the connective tissue surrounding the joint, for there is no well-differentiated joint capsule. Over the dense fibro-cartilaginous tissue of the labrum only the stratum intimale is developed, for subsynovial tissue and blood vessels are absent. Other reptiles agree with *Emys* in the structure of their joints, including the primitive form *Sphenodon* (Haines, 1939, 1940; the animal figured by Lubosch, 1910, as '*Hatteria*' is, judging from the structure of its bone, a species of *Varanus*: see Haines, 1942*b*) and also numerous lizards, crocodiles and chelonians figured in the literature.

On the other hand, the urodele amphibians show much simpler types of joint; some of the larger and proximal joints are eudiarthrodial, while less complicated joints are found in the more distal parts of the limbs, particularly in the extremely neotenic forms such as *Proteus*, in which the phalanges may be joined by hyaline cartilage (Lubosch, 1910, 1938). But Schwarz (1935) has already given good reasons for considering such forms specialized even among the urodeles themselves, and the evolutionary changes that have led to the development of a tough, flexible type of animal from a more rigid and more bony type seem to have included with the reduction of dermal armour and of endochondral bone (Haines, 1942*b*) a simplification of the joints. Certainly the urodeles can no longer be expected to exemplify the more primitive types of joint structure.

THE SIGNIFICANCE OF THE JAW JOINT

Considering the evidence from Dipnoi, *Polypterus* and Holostei, there can be little doubt that one joint, the jaw joint, is always highly differentiated, and that this was also the case in the ancestors of these bony fishes. Further evidence on this problem would perhaps be obtained from a study of the living coelacanth of South Africa. The conclusion is reached that the jaw joint has led the way in joint evolution, being fully developed in Silurian times, when the bony fishes diverged into the various groups discussed (Holmgren & Stensiö, 1936), and that the other joints have followed the jaw joint in their progressive evolutionary development. Probably in any fish there is a potentiality for the development of a eudiarthrosis whenever a joint reaches a sufficient size and degree of movement, as for instance in the fin joint of *Amia*, but in the more primitive types the jaw joint alone satisfied these conditions, for the early semionotids, for instance, which include the ancestors of *Amia*, were all small fishes not more than 15 in. long (Brough, 1936).

This unexpected evolutionary precocity of the jaw joint suggests that eudiarthroses may be as old as the jaws and originally developed in association with them. The basic classification of vertebrates rests on the divergence of Agnatha, with, originally, a suctorial or sieving type of nutrition, and gnathostomes, with well-developed large jaws, particularly in early types, leading a predatory type of existence involving the capture of large prey by snapping jaws. There are no primitive gnathostomes now surviving, but the large ossified or calcified jaws of several of the early placoderms suggest the existence of a well-developed joint for Meckel's cartilage (Moy-Thomas, 1939). Hence it is possible that a fully developed jaw joint is a primitive inheritance of the Gnathostomata.

SUMMARY

1. Contrary to the usual opinion, eudiarthrodial joints with a single joint cavity and a fully developed synovial membrane similar to those of tetrapods are found in the more primitive types of bony fishes, including Dipnoi, *Polypterus* and Holostei, particularly in the jaw joint.

2. In tetrapods this type of joint, inherited from their piscine ancestors, has extended to include even the smaller joints of the limbs.

3. Eudiarthrodial joints were probably first developed in the common ancestors of the bony fishes in Silurian times, and may have been an essential part of the jaw mechanism that differentiated the Gnathostomata from the Agnatha.

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KEY TO LETTERING

Bone is shown black, cartilage white and calcified cartilage stippled

a.fb.c. articular fibro-cartilage
Art. articular bone
b.v. blood vessel
cal.ct. calcified cartilage
fb.ct. fibro-cartilage
hyl.ct. hyaline cartilage
jt.cav. joint cavity
l.c.t. loose connective tissue
lab. labrum
Meck. Meckel's cartilage
p.c.t. perichondral tissues
Quad. quadrate
Rt.a. retro-articular bone
sd.c.t. strand of connective tissue
st.in. stratum intimale
st.ss. stratum subsynoviale

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