nesium-poor. Therefore one may speculate that the planktonic skeleta are first recrystallized to magnesium-rich calcite, with a matrix of similar composition; and that with time this metastable mineral may invert to magnesium-poor calcite.

In contrast, isotopic data show that the recrystallized Cretaceous reef material at Cape Johnson and Hess Guyot was lithified in shallow, warm water, or perhaps subaerially (Table 3). The fact that these limestones have remained in disequilibrium with the ambient deep water suggests that once they are recrystallized there is little tendency toward reequilibration with the new conditions. Sample MP 33-C, from Hess Guyot, does not appear to have recrystallized, so that its Foraminifera still display the $O^{18}:O^{16}$ ratios of the warm surface waters.

Admittedly this concept of submarine lithification raises many questions that remain unanswered. Perhaps most puzzling are the process of recrystallization itself and the (presumably) inorganic precipitation of magnesium-rich calcite in relatively deep water.

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Electron Microscopy: Attachment Sites between Connective Tissue Cells

Abstract. *Regions of attachment have been observed between connective tissue cells from four different structures: fibroblasts in embryonic and fetal tendons, fibroblasts in fetal ligamentum nuchae, odontoblasts, and osteoblasts. Morphologically these sites appear to be focal and to consist of an approximation of the plasma membranes of adjacent cells to within approximately 200 Å. In the region of approximation both the extracellular space and the cytoplasm adjacent to the plasmalemma are increased in density. We have postulated a role for these sites in the maintenance of structural integrity.*

Functional sites of attachment between epithelial cells have been recognized for some time. The attachments of epithelial cells observed with the light microscope have been further defined with the electron microscope and in many epithelia have been subdivided into a junctional complex consisting of three distinct regions: (i) The tight junction (*zonula occludens*), a region in which the outer components of the unit membranes of opposing cells appear to fuse and to act as a seal preventing passage of substances between cells. (ii) An adherent or intermediate zone (*zonula adherens*) in which the plasma membranes of adjacent cells approach each other within a distance of approximately 200 Å. In these regions the space between the cells appears to be of increased density, as does the cytoplasm immediately subjacent to the plasma membrane; these two zones appear to represent continuous circumferential attachment regions between cells. (iii) A desmosome, an attachment plaque (*macula adherens*), ellipsoidal in shape, that appears to be analogous to a "spot weld" between adjacent cells (*1*).

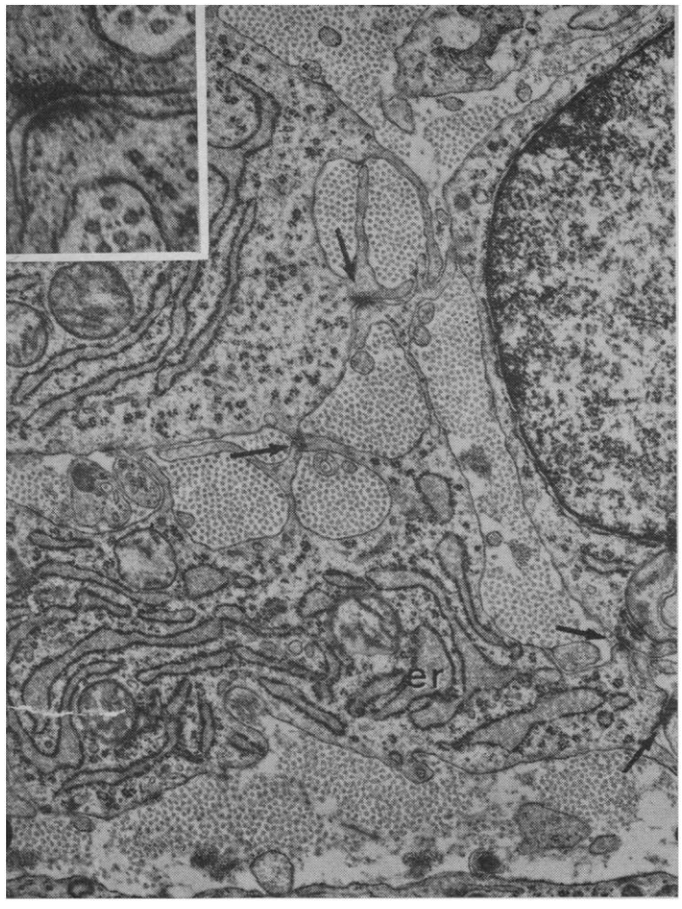
No similar regions of cell attachment have been reported between connective tissue cells in vivo, except for the nexus between adjacent smooth muscle cells (*2*). We have made numerous observations of specific regions of attachment between developing connective tissue cells.

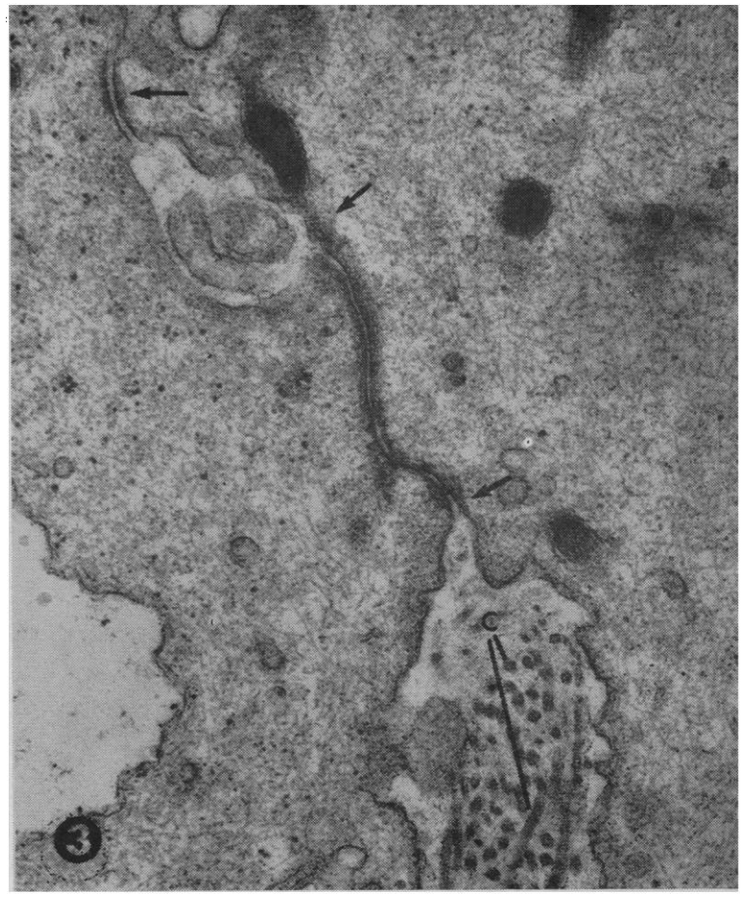
We fixed all tissues in 2 percent osmium tetroxide (*p*H 7.4) buffered with *s*-collidine (*3*). Some of the tissues were further fixed in neutral buffered formalin. They were then dehydrated in a graded series of alcohols, embedded in epoxy resin (*3*), sectioned, stained with uranyl acetate and lead, and examined in an RCA-EMU 3 G electron microscope.

We have repeatedly and consistently observed a region of cell specialization and attachment in developing connective tissue cells from several different sources. These sites consist of an approximation of the plasma membranes of adjacent cells to within a distance of approximately 200 Å. In these regions both the extra-cellular space and the cytoplasm immediately adjacent to the plasma membranes are increased in density. The density of the cytoplasm is often due to numerous, fine filaments at these sites. Such attachment sites occur between fibroblasts from fetal rat tendon (Fig. 1), between those of fetal bovine ligamentum nuchae (Fig. 2), between odontoblasts in the tooth buds of rat embryos (Fig. 3), and between osteoblasts. In the fibroblasts of both the tendon and ligamentum nuchae and in the osteoblasts, these attachment sites appear to be macular or delimited to relatively short distances, whereas in the odontoblasts they were much longer. No highly specialized structures analogous to either the tight junctions or the desmosomes observed in various epithelia were ever seen between any of these connective tissue cells.

During the formation of the digital flexor tendon in the rat, the tendon fibroblasts are continually displaced by the accumulation and enlargement of intercellular collagen fibrils. As these cells are forced apart, they remain attached by relatively long, slender cytoplasmic processes at the end of which are zones of attachment.

Odontoblasts (*4*) in developing tooth buds are attached by similar regions both near their apexes and close to their bases. No such attachment sites





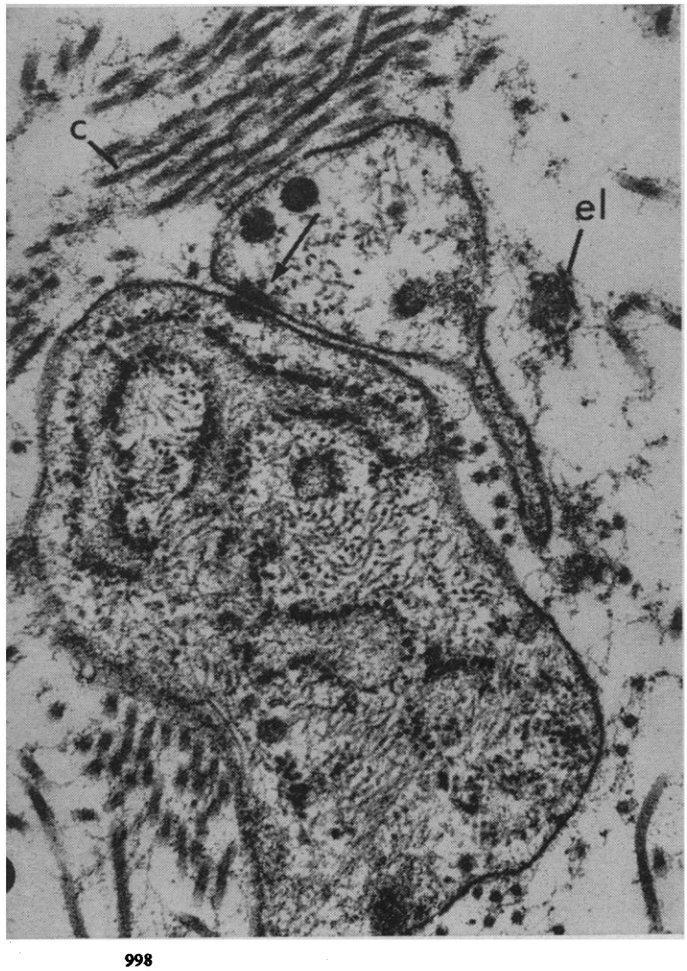


Fig. 1. Electron micrograph of three fibroblasts in a portion of a cross-section of a developing flexor digital tendon of an 18-day-old fetal rat. Part of the large nucleus of one of them and numerous cisternae of rough endoplasmic reticulum (*er*) can be seen within the fibroblasts. These cells send out fine, tubule-like cytoplasmic processes that contact each other at numerous regions. In many of these sites (arrows), a region of increased density can be seen immediately subjacent to the plasma membrane of the cells and between the cells. A higher magnification of one of these regions is seen in the insert. The extracellular spaces contain large numbers of collagen fibrils cut in cross-section, as well as finer fibrils (× 16,000; insert, × 65,000).

Fig. 2. Micrograph of portions of two cells from the developing ligamentum nuchae of a 3-month-old bovine fetus. One of the fibroblasts has numerous cisternae of rough endoplasmic reticulum as well as many fine, cytoplasmic filaments cut both in cross-section and longitudinally. In the extracellular spaces, collagen fibrils can be seen in cross and longitudinal section (*c*), and a portion of a developing elastic fiber can be seen (*el*) to consist of small, tubular fibrils with a dense central matrix. A region of cell contact between these two cells (arrow) consists of cytoplasm immediately adjacent to the membranes and extracellular spaces between the two cells in these regions which are increased in density (× 40,000).

Fig. 3. Electron micrograph taken near the apical region of two neighboring odontoblasts from a developing molar tooth bud of a rat embryo. In this area the cells are relatively free of organelles except for occasional dense bodies and numerous fine, cytoplasmic filaments. Collagen fibrils (*c*) are characteristically located beyond the apical border of the cells and are found here between two cells adjacent to the odontoblastic processes that extend into the dentine. Two regions of cell contact can be seen, the longest of which is delimited by two arrows. These appear as regions of increased density and are suggestive of fibrillar accumulations in the cytoplasm adjacent to the plasma membrane as well as of increased density between the cells. More basally, this cell has the characteristics of other cells which synthesize collagen, that is, an extensive, rough endoplasmic reticulum, Golgi apparatus, and so forth (× 40,000).

could be seen in other regions of neighboring odontoblasts. As the cells migrate toward the pulp away from the forming dentin, they appear to remain attached at these junctional sites.

We have not observed these regions of attachment between fibroblasts in healing wounds or between chondroblasts. In the former the cells are actively motile until wound repair is complete, and in the latter the cells appear to be isolated by the cartilaginous matrix.

The terminology of cell contacts is not yet standardized, and it is possible that the terms used for the specialized regions of the junctional complexes of epithelia may require modification when they are applied to other tissues. The sites of contact between the connective tissue cells noted above are focal, and, like epithelial desmosomes, appear to function as structural intercellular attachments. However, they do not share the morphologic characteristics of epithelial desmosomes, such as intercellular lines, and the characteristic dense layer and looping filaments found subjacent to the plasmalemma (*1*). Rather, they are more similar in appearance to the intermediate junction (*zonula adherens*) described for epithelial cells, although they are not continuously circumferential in the connective tissue cells, with the possible exception of being so in the odontoblast.

One report of tight junctions (*zonula occludens*) between fibroblasts grown in culture has appeared (*5*). We have not observed such regions in any of the cells we studied.

The sites of attachment between connective tissue cells probably play a role in the maintenance of tissue architecture and of intercellular relationships.

Our observations of these regions may be important in understanding subtle differences in the functions of these cells in forming many of the specialized connective tissue structures.

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Intracranial Mobility in the Coelacanth

Abstract. *Analysis of the jaw mechanism of the coelacanth* Latimeria *shows that the action of the intracranial articulation and the associated subcephalic muscles (a system unique to the Crossopterygii) is important in increasing the angle of the gape and the power of the bite. Maximum rotation at the intracranial joint is approximately 15 degrees.*

Discovery of the living coelacanth *Latimeria chalumnae* Smith in 1939 had special significance for students of the problem of the origin of tetrapod vertebrates, because of the close relation of the Coelacanthini to the extinct Rhipidistia—the group of fishes from which the first terrestrial vertebrates arose (*1*).

Among the most interesting features of the cranial anatomy of *Latimeria* is the presence of a joint dividing the braincase into two distinct portions (ethmosphenoid and otico-occipital). A similar intracranial joint is present in all fossil members of the Crossopterygii. A complex system of muscles and ligaments, including special subcephalic muscles innervated by the tenth cranial nerve, is associated with the intracranial articulation in *Latimeria* (*2*), and the tip of the large persistent notochord inserts upon the postero-ventral margin of the ethmosphenoid division of the braincase (another unique feature of crossopterygian fishes).

The function of the intracranial articulation in Crossopterygii has long intrigued paleontologists. Some have suggested that the joint was incapable of movement, even in Devonian Rhipidistia; but most have believed that such a prominent and persistent structure must have had well-defined adaptive and functional significance (*3*). Hitherto the function of the intracranial joint could not be explained by study of the available material of *Latimeria* since all specimens had been fixed in preservative, with immobilization of all muscles and ligaments. Recently, however, I obtained a specimen that had been frozen immediately after capture (*4*).

This specimen measures 107 cm in standard length and weighed 15.87 kg when fresh; its scales indicate an age of about 8 years. Motion and still pictures were made of the range of possible movements of the various skull components immediately after the specimen had thawed; I report the following results:

1) The ethmosphenoid division of the skull can be rotated through a maximum angle of approximately 15 deg relative to the otico-occipital division.

2) The "normal" position of the skull as the gape is closed is such that the ethmosphenoid division of the braincase is in its most ventral position (Fig. 1*A*). At this point the line of the gape from the jaw articulation to the tip of the snout is approximately 27 deg from the horizontal.

3) As the lower jaws are depressed and the gape is opened by simulation of the action of the coraco-mandibular muscles, movement is also produced at the intracranial joint. When the gape is opened to what seems at first to be its maximum extent (approximately 22 deg), the ethmosphenoid has rotated dorsally through approximately 8 deg (*5*); thus the lower jaw has been depressed through some 14 deg (Fig. 1*B*).

4) With the gape open in this position, the cheek can be expanded and contracted in a manner typical of all bony fishes.

5) If further pressure is applied to the lower jaws, the ethmosphenoid is caused to rotate further dorsally. Simultaneously, the quadrate region is moved forward and slightly downward, since the palatoquadrate arch moves as a unit with the ethmosphenoid division of the skull; thus the lower jaws are extended forward. As a result of this new mechanism the gape is increased to approximately 40 deg, 7 deg of the increase resulting from the dorsal rotation of the ethmosphenoid (Figure 1*C*).

6) In order to return the skull to the first position with the gape closed, one must both adduct the lower jaws and retract the ethmosphenoid; that is to say, it is necessary to simulate the action of both the adductor mandibulae and the subcephalic musculature.

7) It was notable that no move-