Development of the Human Temporomandibular Joint

J.R. MÉRIDA-VELASCO,[1]* J.F. RODRÍGUEZ-VÁZQUEZ,[1]
J.A. MÉRIDA-VELASCO,[2] I. SÁNCHEZ-MONTESINOS,[2] J. ESPÍN-FERRA,[2]
AND J. JIMÉNEZ-COLLADO[1]
[1]Departamento de Ciencias Morfológicas II, Instituto de Embriología,
Universidad Complutense, 28040 Madrid, Spain
[2]Departamento de Ciencias Morfológicas, Facultad de Medicina,
Universidad de Granada, Madrid, Spain

ABSTRACT

A great deal of research has been published on the development of the human temporomandibular joint (TMJ). However, there is some discordance about its morphological timing. The most controversial aspects concern the moment of the initial organization of the condyle and the squamous part of the temporal bone, the articular disc and capsule and also the cavitation and onset of condylar chondrogenesis.

Serial sections of 70 human specimens between weeks 7 and 17 of development were studied by optical microscopy (25 embryos and 45 fetuses). All specimens were obtained from collections of the Institute of Embryology of the Complutense University of Madrid and the Department of Morphological Sciences of the University of Granada.

Three phases in the development of the TMJ were identified. The first is the blastematic stage (weeks 7–8 of development), which corresponds with the onset of the organization of the condyle and the articular disc and capsule. During week 8 intramembranous ossification of the temporal squamous bone begins. The second stage is the cavitation stage (weeks 9–11 of development), corresponding to the initial formation of the inferior joint cavity (week 9) and the start condylar chondrogenesis. Week 11 marks the initiation of organization of the superior joint cavity. And the third stage is the maturation stage (after week 12 of development).

This work establishes three phases in TMJ development: 1) the blastematic stage (weeks 7–8 of development); 2) the cavitation stage (weeks 9–11 of development); and 3) the maturation stage (after week 12 of development). This study identifies the critical period of TMJ morphogenesis as occurring between weeks 7 and 11 of development. Anat Rec 255:20–33, 1999. © 1999 Wiley-Liss, Inc.

In the last few decades a considerable amount of research has been published on the development of the temporomandibular joint (Harpman and Woollard, 1938; Symons, 1952; Moffett, 1957; Van Dongen, 1968; Perry et al., 1985). Studies have focused on the development of the articular disc and its relation with the lateral pterygoid muscle (Yuodelis, 1966a; Wong et al., 1985; Smeele, 1990; Mérida Velasco et al., 1993; Ögütcen-Toller and Juniper, 1993, 1994); the development of bony articular elements (Baume, 1962; Yuodelis, 1966b; Baume and Holz, 1970; Bach-Petersen et al., 1993); and the relationship between the temporomandibular region and the middle ear (Coleman, 1970; Smeele, 1988; Rodríguez Vázquez et al., 1992, 1993; Ögütcen-Toller, 1995). However, few of these studies have attempted to systematize chronologically the morphological changes taking place in the temporomandibular joint during development.

Van der Linden et al. (1987) studied 52 human embryos and fetuses, establishing the critical period of TMJ morphogenesis between weeks 7 and 11 of development. Moreover, Morimoto et al. (1987) describes a number of phases in

*Correspondence to: Prof. Dr. J.R. Mérida Velasco, Departamento de Ciencias Morfológicas II, Facultad de Medicina, Universidad Complutense, 28040 Madrid, Spain.
E-mail: jfrodvaz@eucmax.sim.ucm.es

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TABLE 1. Features of the specimens used

	C-R length (mm)	Plane of section	O'Rahilly stage*	Weeks of development
Embryos				
E-1	21	Frontal	21	7
GI-14	21	Transverse	21	7
R-1	21	Transverse	21	7
GV-6	22	Frontal	21	7
MOM	22	Frontal	21	7
MA-7	22	Transverse	21	7
X-6	22.5	Transverse	21	7
F	23	Transverse	22	7
NO-15	23	Frontal	22	7
Pe-8	23	Transverse	22	7
CH-1	24	Transverse	22	7
X-14	24	Transverse	22	7
EA-3	24.5	Sagittal	22	7
PT-3	26	Frontal	22	7
BB-4	26	Transverse	22	7
GIV-4	26.5	Frontal	22	7
Mes-2	27	Frontal	22	7
Br-4	28	Frontal	23	8
C-11	28	Transverse	23	8
P-1	29	Frontal	23	8
NA-1	29	Transverse	23	8
Ca-2	29	Transverse	23	8
LR-7	30	Transverse	23	8
BB-2	30	Transverse	23	8
X-14	30	Transverse	23	8
Fetuses				
Ca-1	35	Transverse		9
Fe	35	Frontal		9
Pe	35	Transverse		9
Ba-1	36	Frontal		9
Me-1	37	Transverse		9
O-1	38	Frontal		9
OY-2	38	Frontal		9
OY	38	Sagittal		9
Be-2	39	Transverse		9
OC	43	Frontal		10
JR-3	43	Frontal		10
VR-2	45	Frontal		10
C-17	45	Frontal		10
LR-6	46	Frontal		10
Be	47	Sagittal		10
Be-503	48	Frontal		10
Ca-6	52	Frontal		11
JR-1	55	Frontal		11
JP-1	56	Transverse		11
Fe-21	57	Transverse		11
B-52	57	Frontal		11
Be-101	65	Frontal		11
Bu-19	66	Transverse		12
Ri-11	69	Transverse		12
Be-113	70	Frontal		12
F-1	72	Frontal		12
HL-30	74	Transverse		12
JR-8	75	Frontal		12
Ca-7	76	Transverse		12
JR-6	80	Frontal		12
B-516	82	Sagittal		13
Be-3	83	Transverse		13
J-1	86	Sagittal		13
B-54	91	Transverse		13
Bu-18	93	Transverse		13
B-207	95	Frontal		13
B-195	97	Transverse		13
ZO	102	Sagittal		14
Be-1010	103	Transverse		14
Bu	113	Transverse		14

TABLE 1. Features of the specimens used (continued)

	C-R length (mm)	Plane of section	O'Rahilly stage*	Weeks of development
Fetuses (continued)				
Ce-2	115	Transverse		14
R-6	125	Transverse		15
Cu-2	137	Frontal		16
Esc-3	139	Transverse		16
B-28	150	Transverse		17

*Stages are given though stage 23 (8 weeks), the end of the embryonic period, which is as far as the staging system extends. Beyond 8 weeks, only weeks are indicated.

TMJ development. During the TMJ "appearance stage" (weeks 8–9 of development) he observed the glenoid and condylar blastemata. In the TMJ "preliminary stage" (weeks 10–17 of development) the articular disc and the joint cavities are formed as well as synovial tissue, while the condyle shows cartilage and endochondral ossification. Finally, in the TMJ "completion stage" (week 21 to term), all articular elements undergo growth and hematopoiesis begins.

The aim of this work is to study the development of the temporomandibular joint in human specimens between weeks 7 and 17 of development and to throw some new light onto the chronology of the sequence of events taking place. This joint is of particular interest because of its complex development in relation to structures in the middle ear (Meckel's cartilage, discomalleolar ligament) as well as its clinical importance. It is necessary to increase our knowledge on the organization of this structure for a better understanding of the craniofacial anomalies which affect this region.

MATERIALS AND METHODS

For this study 70 human specimens (25 embryos and 45 fetuses) from collections of the Institute of Embryology of the Complutense University of Madrid and the Department of Morphological Sciences of the University of Granada were used.

Crown-rump (C-R) length, plane of section, and stage of development for the embryonic period (O'Rahilly and Müller, 1987) are shown in Table 1. The usual laboratory procedures were used to prepare 10–20 µm thick transverse, frontal or sagittal serial sections, which were stained with haematoxylin-eosin and azocarmine (McManus and Mowry, 1968) for light microscopic study.

RESULTS

Week 7

During week 7 (O'Rahilly's stages 21 and 22), mesenchymal condensation was observed in the temporomandibular joint region upon the future mandibular ramus. This condensation corresponded to the condylar anlage. The blastema of the lateral pterygoid muscle was associated with the superior internal portion of the condylar anlage (Fig. 1a).

The condylar anlage was associated with the masseteric and auriculotemporal nerves. The auriculotemporal nerve ran between the future condyle and Meckel's cartilage (Fig. 1a).

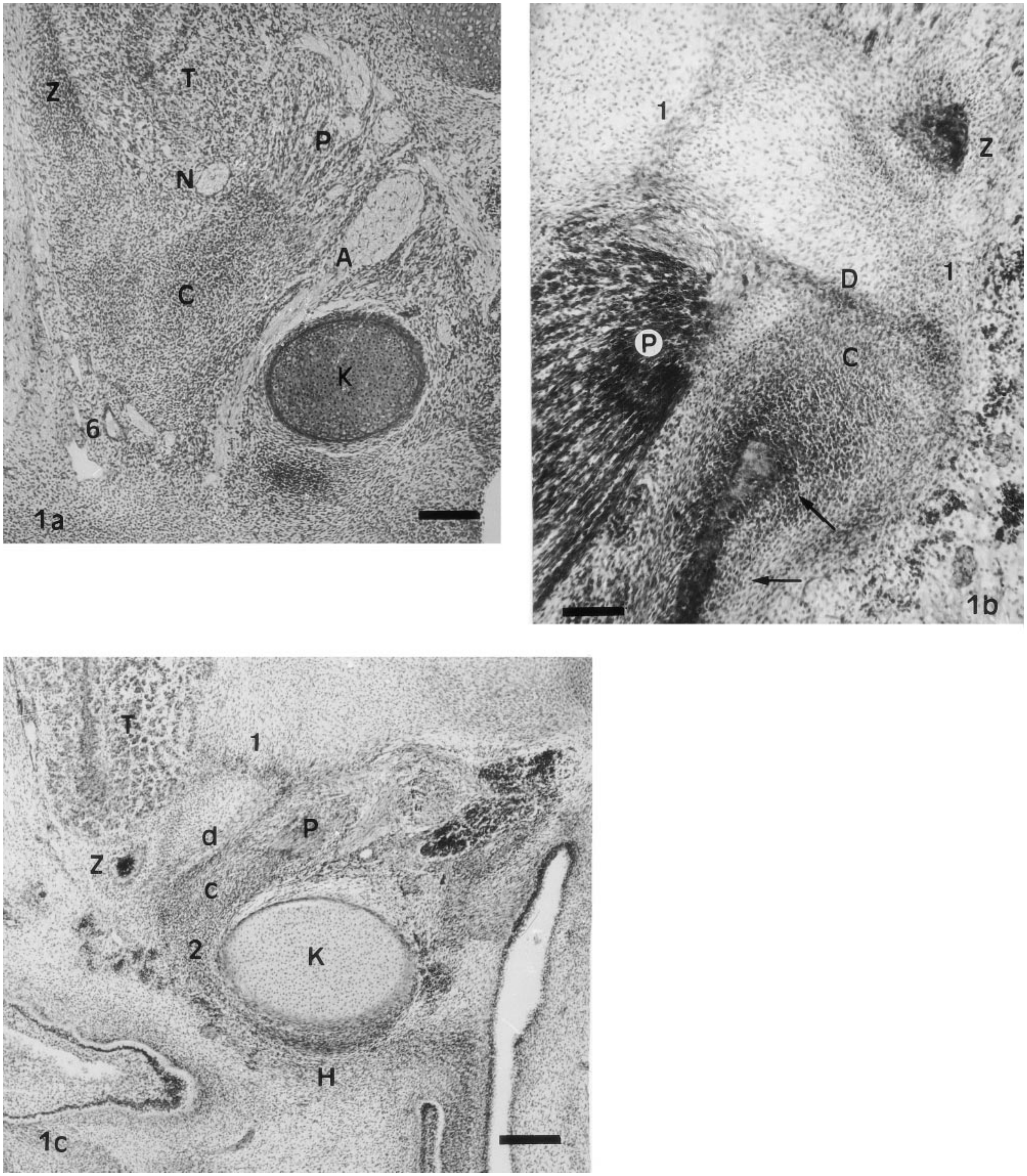


Fig. 1. Blastematic stage. **a:** Human embryo GIV-4 (26.5 mm C-R; week 7 of development; O'Rahilly stage 22). Frontal section. The condylar blastema (C) was associated with the lateral pterygoid muscle (P). A, auriculotemporal nerve. K, Meckel's cartilage. Z, zygomatic process of the squamous part of the temporal bone. N, masseteric nerve. T, temporalis muscle. 6, superficial temporal artery. Scale bar = 200 µm. **b:** Human embryo Br-4 (28 mm C-R; week 8 of development; O'Rahilly stage 23). Frontal section. The zygomatic process (Z) of the squamous part of the temporal bone begins its intramembranous ossification. Arrows, the intramembranous ossification of the mandibular ramus. P, lateral pterygoid muscle. C, condylar blastema. D, articular disc. 1, articular capsule. Scale bar = 200 µm. **c:** Human embryo P-1 (29 mm C-R; week 8 of development; O'Rahilly stage 23). Frontal section of the posterior joint region. The anlage of the discomalleolar ligament is visible (2). The discomalleolar ligament is associated with the Meckel's cartilage (K) and with the mesenchymal condensation of the tympanic bone (H). Z, zygomatic process of the squamous part of the temporal bone. P, lateral pterygoid muscle. 1, articular capsule. T, temporalis muscle. d, articular disc. c, condylar blastema. Scale bar = 200 µm.

A mesenchymal condensation appeared craniolaterally to the condylar anlage that formed the blastema of the zygomatic process of the squamous part of the temporal bone (Fig. 1a).

Temporal and condylar blastemas were separated by lax mesenchymal tissue.

Week 8

During week 8 (O'Rahilly's stage 23), intramembranous ossification of the zygomatic process of the squamous part of the temporal bone began (Fig. 1b).

Intramembranous ossification of the ramus of the mandible reached the base of the future condyle (Fig. 1b). Craniolaterally to the future condyle there was a mesenchymal condensation that formed the anlage of the articular disc (Fig. 1b). There were no joint cavities during this stage. The mesenchymal condensation that formed the anlage of the capsule extended from the squamous part of the temporal bone to the anlage of the disc and condyle (Fig. 1b). The lateral pterygoid muscle inserted in the medial portion of the condylar-discal complex. In the posterior joint region a condensed mesenchymal band could be observed from the area of insertion of the lateral pterygoid muscle to the condylar-discal complex to the lateral surface of Meckel's cartilage. This mesenchymal condensation was the anlage of the discomalleolar ligament (Fig. 1c).

Week 9

The intramembranous ossification of the squamous part of the temporal bone was continuous and no cartilaginous regions were observed. At this week condylar chondrification began in the centre of the condylar blastema (Fig. 2a). Similarly, small spaces or clefts appeared between the anlage of the articular disc and the mandibular condyle that defined the initial formation of the inferior joint cavity (Fig. 2b).

The lateral pterygoid muscle inserted in the condylar-discal complex. The lay-out in the posterior joint region was the same as the previous week.

Week 10

The organization of the inferior joint cavity was complete although crossed by a few tracts of connective tissue. There was still no sign of the superior joint cavity (Fig. 2c). Lateral to the joint capsule which inserted in the external part of the articular disc a number of blood vessels were present.

The condylar cartilage had a conical shape and was surrounded by intramembranous ossification. The base of the condylar cartilage corresponded to the joint region and its vertex was placed next to the future mandibular foramen (Fig. 2d).

In the posterior joint region, intramembranous ossification of the zygomatic process of the squamous part of the temporal bone was observed extending along the vertical part of the squamous region. The discomalleolar ligament was connected to the lateral surface of Meckel's cartilage, tympanic bone and gonial bone. Branches of the anterior tympanic artery appeared laterally to the discomalleolar ligament (Fig. 2e).

Week 11

The organization of the superior joint cavity began between the zygomatic process of the squamous part of the temporal bone and the articular disc (Fig. 2f). The articular surface of the squamous part of the temporal bone had a flat surface.

The joint capsule was situated between the zygomatic process of the squamous part of the temporal bone and the condyle and was attached to the external part of the articular disc (Fig. 2g). The discocapsular complex was ventrally associated with the masseteric nerve (Fig. 2h).

Beneath the lateral ligament of the joint, several branches of the transverse facial artery were visible. In the external portion of the condylar cartilage, adjacent to the insertion of the articular disc, an invagination of mesenchymal cells was observed (Fig. 2g).

The superior fascicles of the lateral pterygoid muscle inserted into the articular disc and mandibular condyle whereas the inferior fascicles of the lateral pterygoid muscle inserted into the mandibular condyle (Figs. 2f, i).

Fig. 2. Cavitation stage. (Page 24.) **a:** Human fetus O-1 (38 mm C-R; week 9 of development). Frontal section. The mandibular condyle (CD) begins its chondrification. Z, zygomatic process of the squamous part of the temporal bone. D, articular disc. P, lateral pterygoid muscle. A, auriculotemporal nerve. K, Meckel's cartilage. Scale bar = 200 µm. **b:** Human fetus O-1 (38 mm C-R; week 9 of development). Frontal section. Enlargement of panel a. Small spaces (arrows) show initial inferior articular cavity formation. D, articular disc. CD, mandibular condyle. Scale bar = 50 µm. **c:** Human fetus Be-503 (48 mm C-R; week 10 of development). Frontal section. The inferior articular cavity (asterisk) continues its organitation between the articular disc (D) and the mandibular condyle (CD). K, Meckel's cartilage. P, Lateral pterygoid muscle. Z, zygomatic process of the squamous part of the temporal bone. CE, bifurcation of the external carotid artery. 1, Articular capsule. T, temporalis muscle. A, auriculo temporal nerve. Scale bar = 200 µm. (Page 25.) **d:** Schematic drawing of the condylar cartilage (CC) during week 10 of development. The medial pterygoid muscle is displaced. The inferior alveolar nerve is located between the medial and lateral laminae of the body of the mandible. NM, mandibular nerve. DI, inferior alveolar nerve covered by the medial lamina of the body of the mandible. LI, lingual nerve. MH, Nerve to mylohyoid. K, Meckel's cartilage. FD, first deciduous molar. TD, second deciduous molar. A, auriculotemporal nerve. **e:** Human fetus Be-503 (48 mm C-R; week 10 of development). Frontal section of the posterior joint region. The intramembranous ossification of the zygomatic process reaches the vertical portion of the squamous part of the temporal bone. Delimitation of the tympanosquamosal fissure between the squamous part of the temporal bone and the tympanic bone. E, squamous part of the temporal bone. H, tympanic bone. G, gonial bone. K, Meckel's cartilage. 2, discomalleolar ligament. Arrow, branch of the anterior tympanic artery. TI, chorda tympani nerve. Scale bar = 200 µm. **f:** Human fetus Be-101 (65 mm C-R; week 11 of development). Frontal section. The superior articular cavity is located between the zygomatic process (Z) of the squamous part of the temporal bone and the articular disc (d). 3, superior fascicles of the lateral pterygoid muscle. 4, inferior fascicles of the lateral pterygoid muscle. A, auriculotemporal nerve. 5, middle meningeal artery. 6, superficial temporal artery. CD, mandibular condyle. N, masseteric nerve. Scale bar = 200 µm. (Page 26.) **g:** Human fetus Be-101 (65 mm C-R; week 11 of development). Enlargement of panel f. 1, articular capsule. L, lateral ligament of the joint. CD, mandibular condyle. Z, zygomatic process of the squamous part of the temporal bone. D, articular disc. Arrow, invagination of mesenchymal cells. 7, transverse facial artery. Scale bar = 200 µm. **h:** Human fetus Be-101 (65 mm C-R; week 11 of development). Frontal section of the anterior joint region. Z, zygomatic process of the squamous part of the temporal bone. CD, Mandibular condyle. N, masseteric nerve. L, lateral ligament of the joint. AM, maxillary artery. P, lateral pterygoid muscle. Scale bar = 200 µm. **i:** Human fetus Be-101 (65 mm C-R; week 11 of development). Frontal section. The superior fascicles of the lateral pterygoid muscle (3) insert (arrow) in the articular disc (D). CD, mandibular condyle. 4, inferior fascicles of the lateral pterygoid muscle. N, masseteric nerve. T, temporalis muscle. Z, zygomatic process of the squamous part of the temporal bone. A, auriculotemporal nerve. AM, maxillary artery. Scale bar = 200 µm.

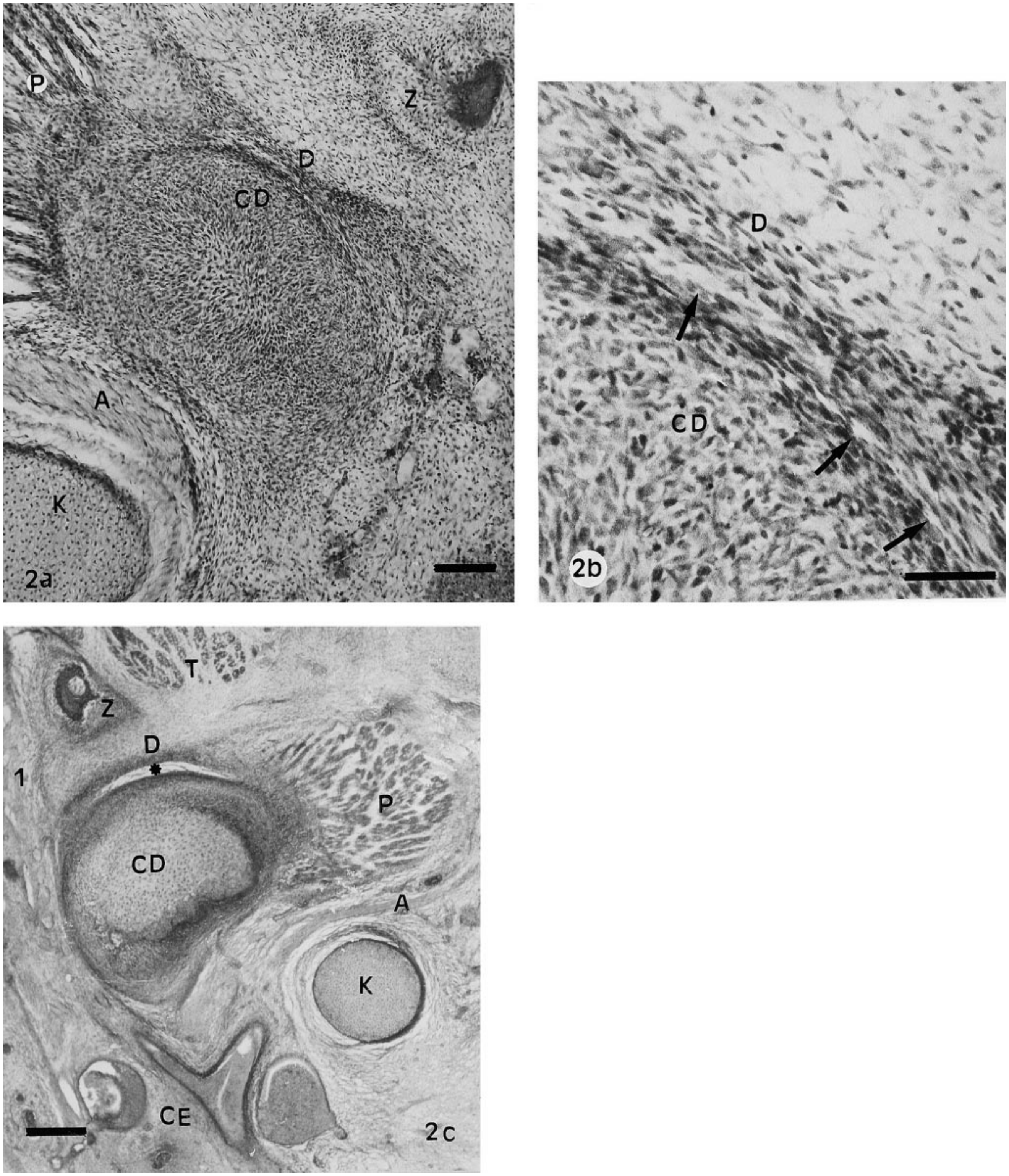


Figure 2 a, b, c.

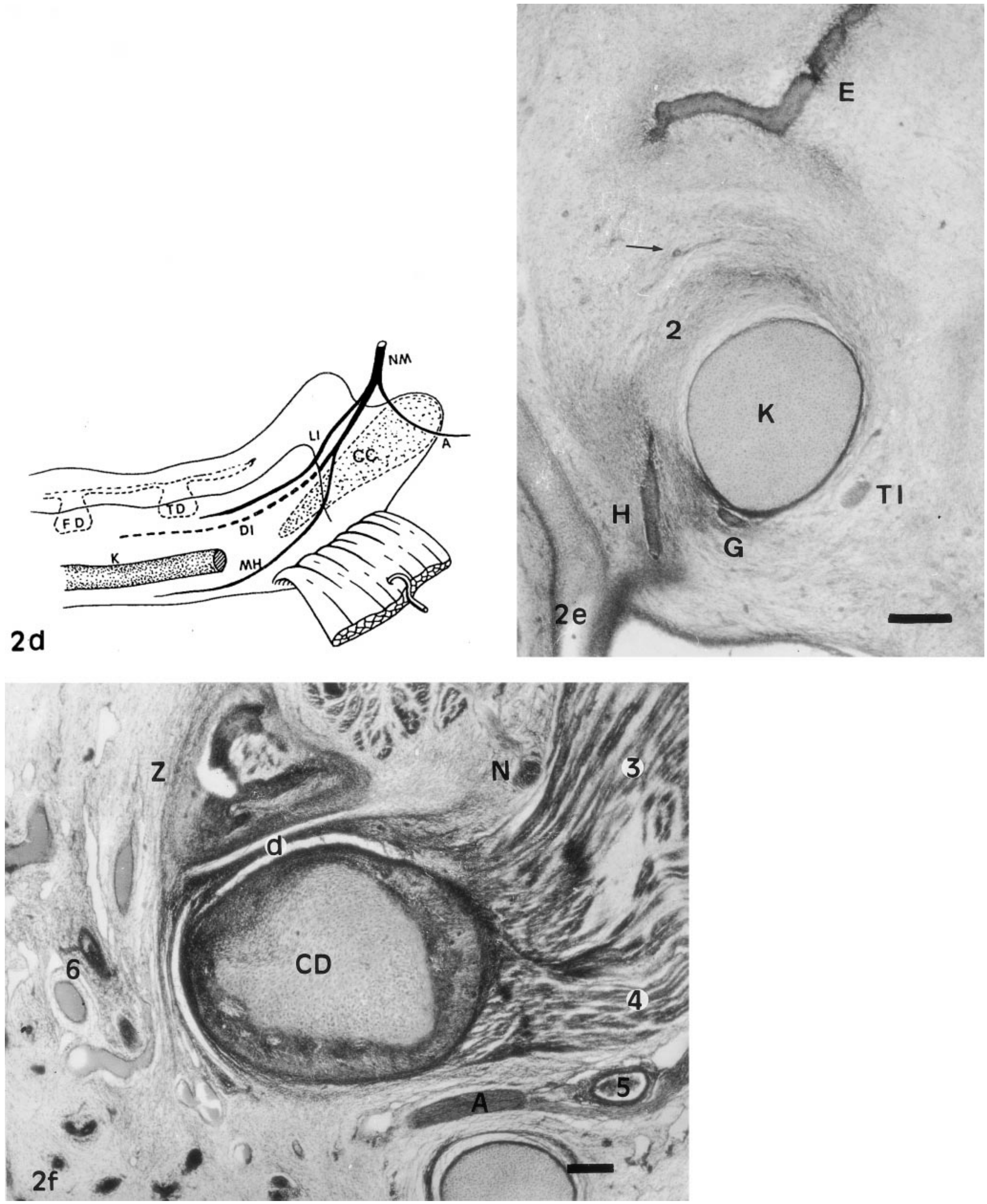


Figure 2 d, e, f.

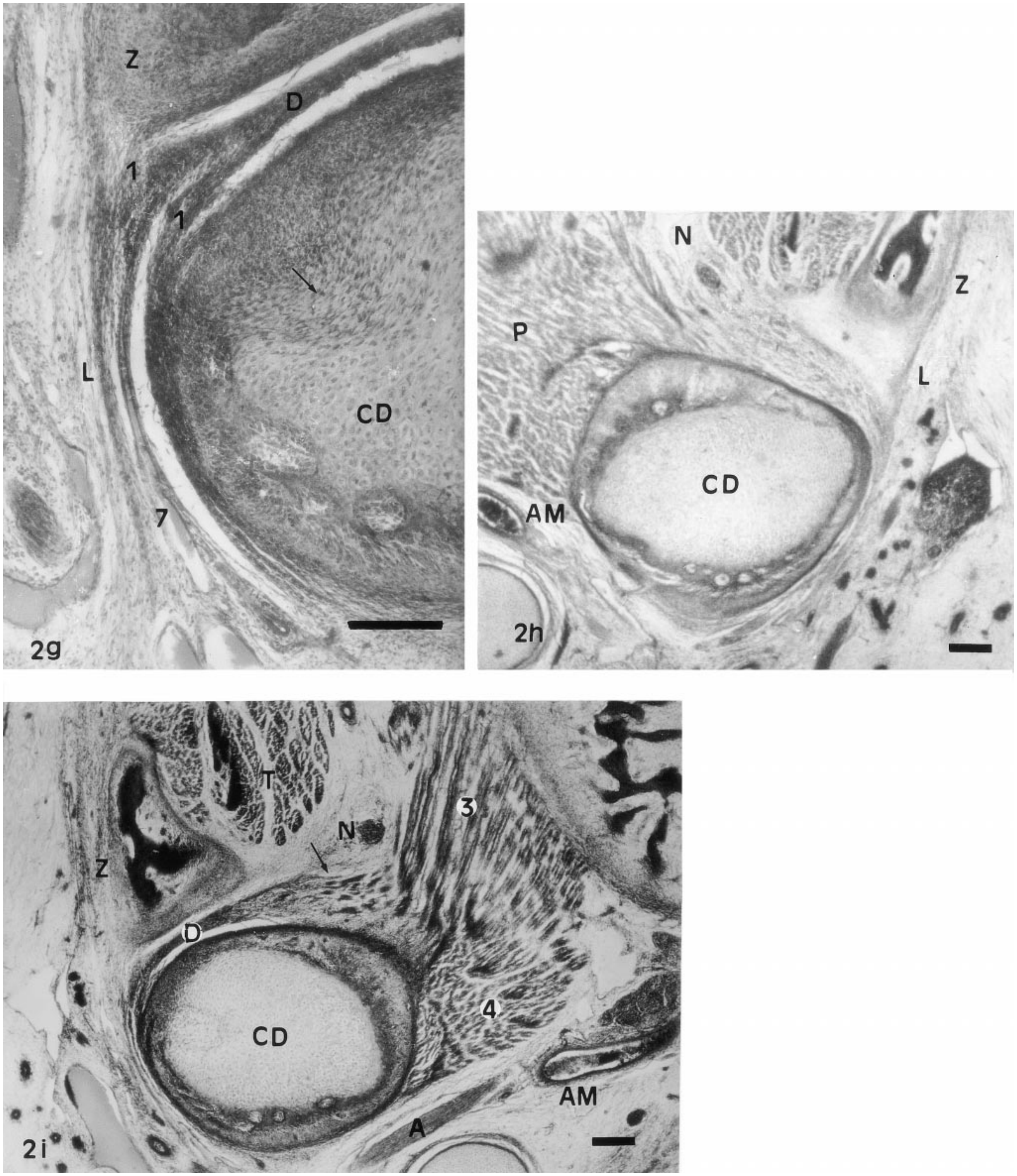


Figure 2 g, h, i.

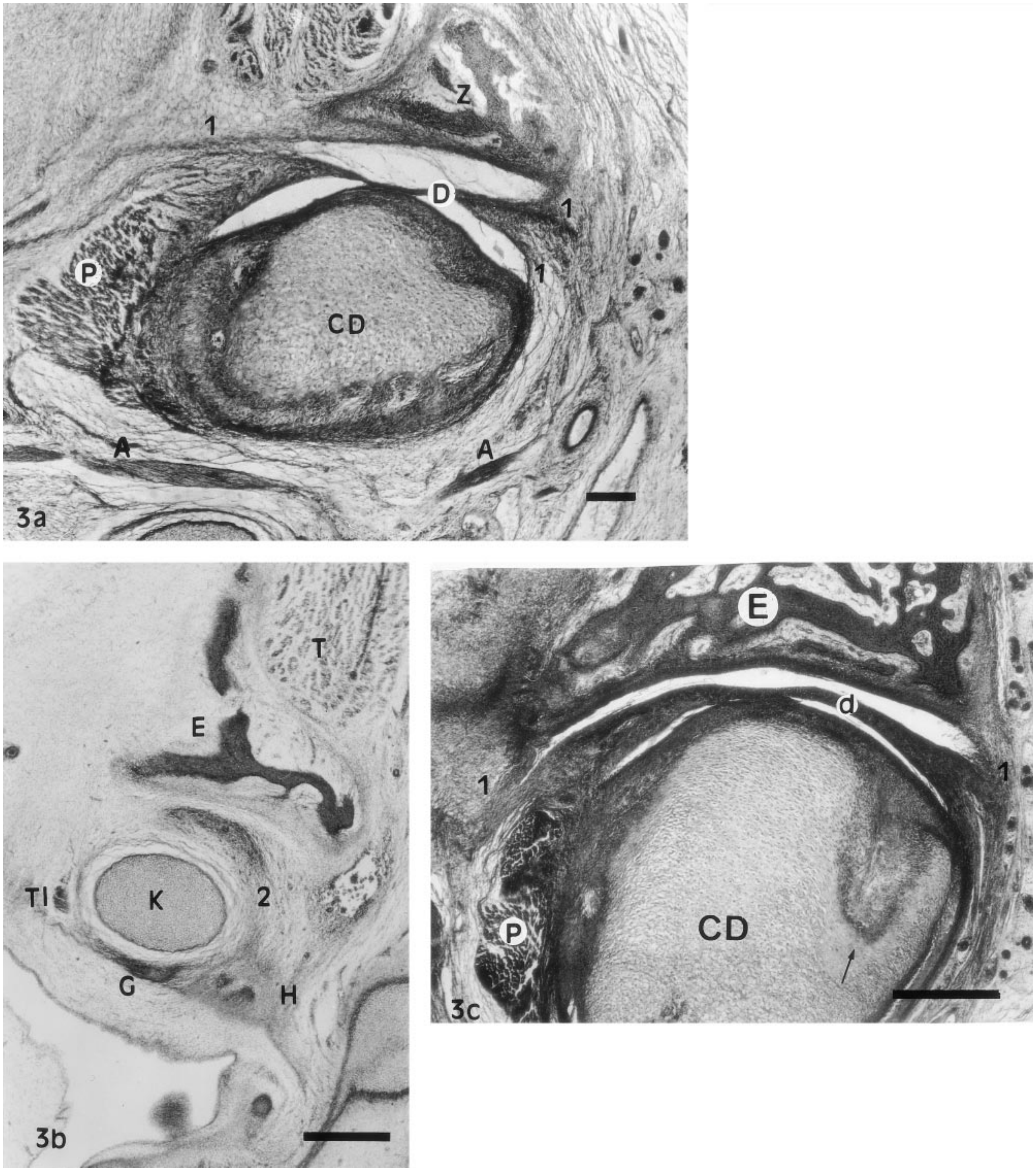
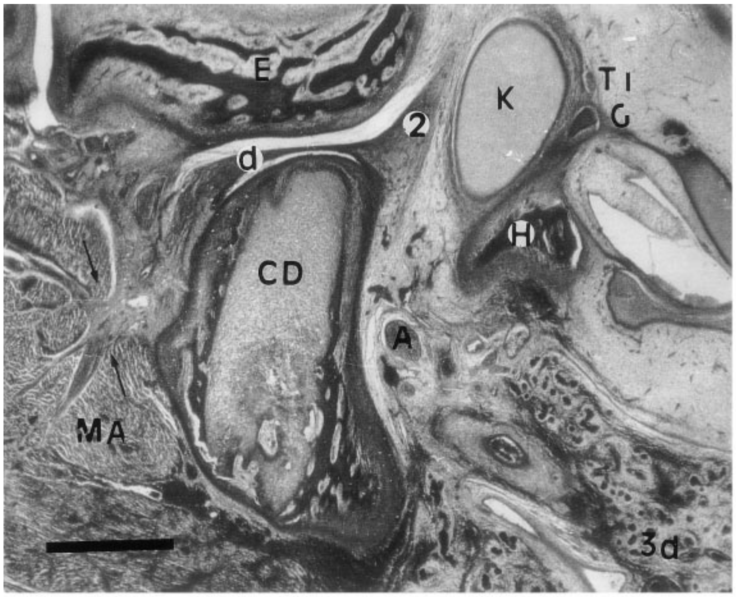


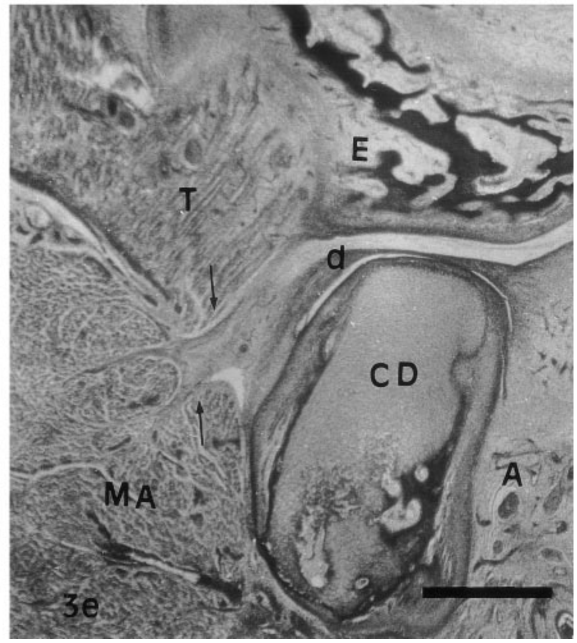
Figure 3 a, b, c. (Legend on page 29.)

Weeks 12 to 17

During this period the organization of the temporomandibular joint system was complete and five events were particularly noteworthy.

1) During week 12, there were no significant changes in the joint surfaces. The joint cavities were clearly defined and a decrease in the number of septa of connective tissue that crossed them was noted (Fig. 3a). Between the squamous part of the temporal bone and the tympanic bone was located the tympanosquamosal fissure through which run the chorda tympani nerve, Meckel's cartilage and the discomalleolar ligament (Fig. 3b).





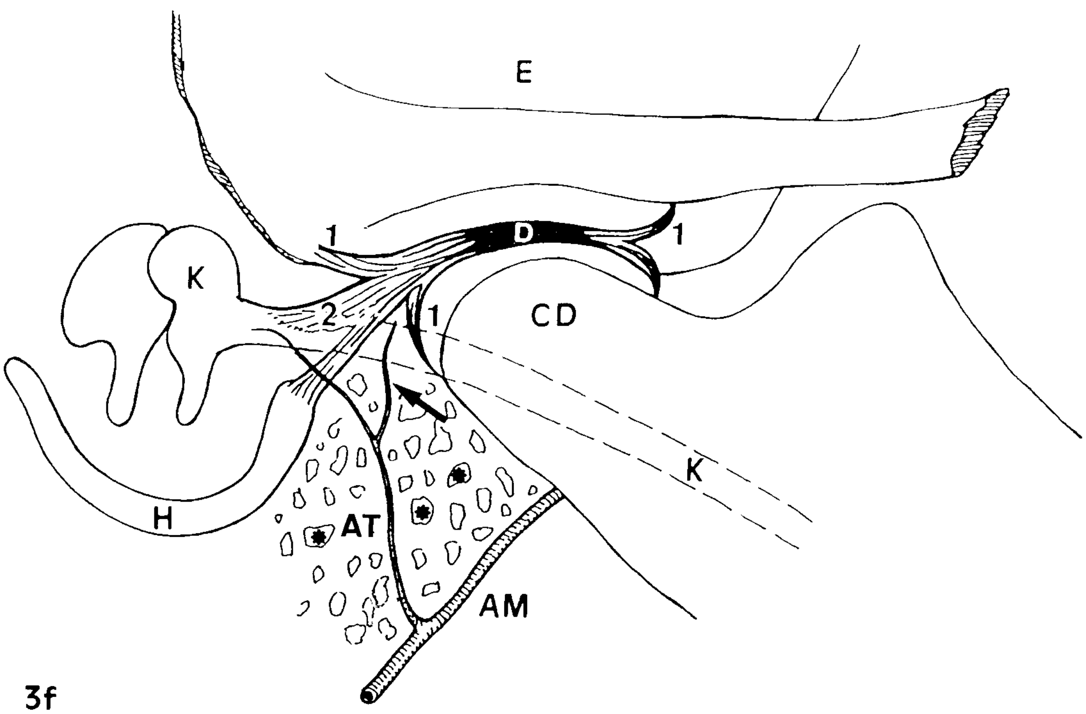


Figure 3 f.

2) By week 13 the joint surface of the squamous part of the temporal bone had acquired a concave morphology (Fig. 3c). The articular disc inserted into the external condylar surface and the invagination of the vascular mesenchyme in the form of septa were observed (Fig. 3c).

Growth of the tympanic bone and the squamous portion of the temporal bone conditions a narrowing of the tympanosquamosal fissure. However, at this phase of development, the inferior border of the tegmen tympani of the petrous part of the temporal bone has not appeared

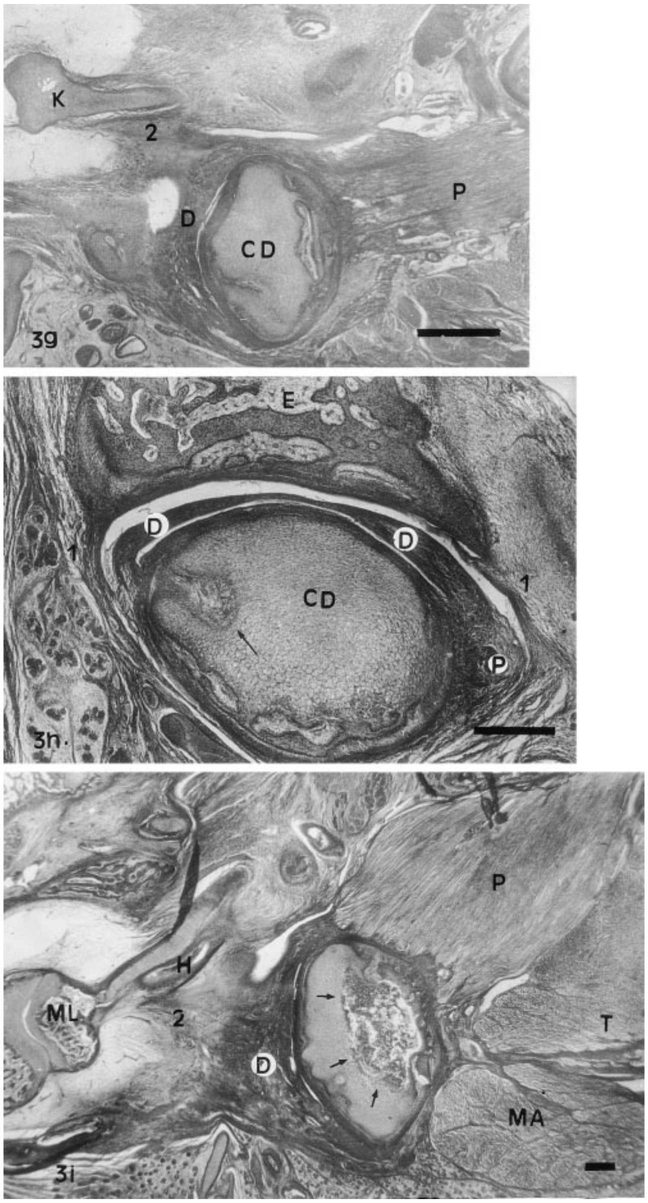


Fig. 3. Maturation stage. **a:** Human fetus JR-6 (80 mm C-R; week 12 of development). Frontal section. The articular capsule (1) is attached to the eccentric margin of the articular disc (D). P, lateral pterygoid muscle. CD, mandibular condyle. Z, zygomatic process of the squamous part of the temporal bone. A, auriculotemporal bone. Scale bar = 200 µm. **b:** Human fetus JR-8 (75 mm C-R; week 12 of development). Frontal section. The tympanosquamosal fissure appears clearly demarcated between the tympanic bone (H) and squamous part of the temporal bone (E). T, temporalis muscle. K, Meckel's cartilage. 2, discomalleolar ligament. G, gonial bone. TI, chorda tympani nerve. Scale bar = 500 µm. **c:** Human fetus B-207 (95 mm C-R; week 13 of development). Frontal section. In the mandibular condyle invagination of the vascular mesenchyme (arrow) is visible. E, squamous part of the temporal bone. d, articular disc. 1, articular capsule. P, lateral pterygoid muscle. CD, mandibular condyle. Scale bar = 500 µm. **d:** Human fetus B-516 (82 mm C-R; week 13 of development). Sagittal section. The chorda tympani nerve (TI), Meckel's cartilage (K), gonial bone (G), and discomalleolar ligament (2) run through the tympanosquamosal fissure. The articular disc shows fibrous projections into the muscle fibers of the masseter muscle (arrows). CD, mandibular condyle. E, squamous part of the temporal bone. H, tympanic bone. MA, masseter muscle. d, articular disc. A, auriculo temporal nerve. Scale bar = 500 µm. **e:** Human fetus B-516 (82 mm C-R; week 13 of development). Sagittal section. The anterior portion of the articular disc (d) shows fibrous projections in to the muscle fibers of the masseter muscle and temporalis muscle (arrows). CD, mandibular condyle. E, squamous part of the temporal bone. MA, masseter muscle. T, temporalis muscle. A, auriculotemporal nerve. Scale bar = 500 µm. **f:** Schematic drawing of the arrangement in the posterior joint region of the articular capsule (1). 2, discomalleolar ligament. CD, mandibular condyle. K, Meckel's cartilage. E, squamous part of the temporal bone. D, articular disc. AT, anterior tympanic artery. Arrow: branch of the anterior tympanic artery. AM, maxillary artery. H, tympanic bone. Asterisk, retrodiscal venous plexus. **g:** Human fetus Ce-2 (115 mm C-R; week 14 of development). Transverse section. Meckel's cartilage (K) has experienced a reduction in volume. 2, discomalleolar ligament. D, articular disc. CD, mandibular condyle. D, lateral pterygoid muscle. Scale bar = 500 µm. **h:** Human fetus Cu-2 (137 mm C-R; week 16 of development). Frontal section. The articular capsule (1) is limiting the lateral recess of the articular cavity. The vascular canals (arrow) enter in to the condylar cartilage. E, squamous part of the temporal bone. CD, mandibular condyle. D, articular disc. P, lateral pterygoid muscle. Scale bar = 500 µm. **i:** Human fetus B-28 (150 mm C-R; week 17 of development). Transverse section. The anterior part of the mandibular condyle shows endochondral ossification (arrows). The discomalleolar ligament (2) is inserted in the malleus (ML) of the middle ear. H, tympanic bone. D, articular disc. P, lateral pterygoid muscle. T, temporalis muscle. MA, masseter muscle. Scale bar = 500 µm.

between the tympanic bone and the squamous part of the temporal bone (Fig. 3d). Therefore, the petrosquamous and petrotympanic fissures have not yet formed. The chorda tympani nerve, the Meckel's cartilage, the gonial bone (Fig. 3d), the discomalleolar ligament and the anterior tympanic artery (Fig. 3f) all proceeded through the tympanosquamosal fissure (Fig. 3d).

During week 13 some fibrous projections can be clearly seen in the anterior portion of the articular disc that were associated with the masseter and temporal muscles (Figs. 3d, e).

The posterior portion of the joint capsule inserts into the squamous part of the temporal bone, the tympanic bone and the posterior surface of the mandibular condyle. The discomalleolar ligament runs between the capsular insertion in the squamous part of the temporal bone and the tympanic bone, towards the middle ear (Fig. 3f). In the retrocapsular space the auriculotemporal nerve (Fig. 3d) and the branch originating from the anterior tympanic artery and the retrodiscal venous plexus can be seen (Fig. 3f).

3) After week 14 there was a clear reduction in the volume of Meckel's cartilage (Fig. 3g).

4) During week 16 the narrow central portion of the articular disc appears avascular although small vessels can be observed on the peripheral portions. Vascular canals can be seen on the external part of the condylar cartilage (Fig. 3h).

5) During week 17 there was a clear endochondral ossification of the anterior portion of the condyle in association with the insertion of the lateral pterygoid muscle (Fig. 3i). The discomalleolar ligament had a fibrous aspect and ran along the tympanosquamosal fissure while the malleus of the middle ear was in an advanced stage of endochondral ossification (Fig. 3i). Table 2 summarizes the most relevant findings of our study.

TABLE 2. Summary of the results

	Week of development										
	7	8	9	10	11	12	13	14	15	16	17
Blastema temporal	X										
Blastema condylar	X										
Intramembranous ossification of the zygomatic process of the squamous part of the temporal bone		X									
Anlage of the articular disc		X									
Anlage of the capsule		X									
Anlage of the discomalleolar ligament		X									
Condylar chondrification			X								
Inferior joint cavity			X								
Superior joint cavity					X						
The joint surface of the squamous part of the temporal bone had adquired a concave morphology							X				
The anterior portion of the articular disc shows fibrous projections in association to the masttcatory muscles							X				
Reduction in volume of meckel's cartilage								X			
Vascular canals in the condylar cartilage										X	
The anterior portion of the mandibular condyle shows endochondral ossification											X

DISCUSSION

Compared with diarthrosis of the extremities, the development of the temporomandibular joint is a relatively late process. The joint cavities of the elbow, hip or knee become visible at week 8 of development (O'Rahilly's stage 23) (Gardner and O'Rahilly, 1968; O'Rahilly and Müller, 1996; Mérida Velasco et al., 1997b), whereas at this stage in the temporomandibular joint region only the mesenchymal condensations of the mandibular condyle, the articular disc and the squamous part of the temporal bone are present and there is still no sign of the joint cavity. Nevertheless, buccal movements can be observed (Humphrey, 1968) which, in the absence of the temporomandibular joint cavity, take place in the joint that exists between the posterior portion of Meckel's cartilage (the future malleus bone) and the cartilaginous form of the future incus (Mérida Velasco et al., 1990; Burdi, 1992).

From our observations we identified three periods in the development of the TMJ: 1) the blastematic stage, weeks 7–8 of development (O'Rahilly's stages 21 to 23); 2) the cavitation stage, between weeks 9 and 11 of development; and 3) the maturation stage, after week 12 of development. Our observations do not agree with those of Morimoto et al. (1987), who observed the TMJ "appearance stage" between weeks 8 and 9; the "preliminary stage" of TMJ development between weeks 10 and 17; and week 21 as the end of TMJ "completion stage." In our observations, the critical period of TMJ morphogenesis occurs in the blastematic and cavitation stages described by us (7–11 weeks of development) (Van der Linden et al., 1987).

During the blastematic stage (week 7) we observed the anlages of the mandibular condyle and zygomatic process of the squamous part of the temporal bone (Yuodelis, 1966a; Moffett, 1977; Van der Linder et al., 1987; Ögütcen-Toller and Juniper, 1994). Symons (1952) describes the zygomatic process anlage in week 8 of development. For Perry et al. (1985), the anlage of the condyle and zygomatic process of the squamus part of the temporal bone begins its formation at week 9. Also, intramembranous ossification of the squamous part of the temporal bone begins during week 8 of development (O'Rahilly's stage 23) (Baume, 1962; Yuodelis, 1966a,b; Baume and Holz, 1970; Sperber, 1989). However, for Van Dongen (1968), Perry et al. (1985), Van der Linden et al. (1987) and Burdi (1992), this process begins during week 10.

Concerning the articular disc, its first sign in our study was as a mesenchymal condensation craniolateral to the condyle (Symons, 1952; Moffett, 1957; Yuodelis, 1966a; Smeele, 1990) in embryos at week 8 of development (O'Rahilly's stage 23). However, Moffett (1977) observed it for the first time in 6-week-old embryos and Van der Linden et al. (1987), Sperber (1989) and Burdi (1992) in specimens of week 7 of development.

We have shown that development of the joint capsule begins in embryos at week 8 of development (O'Rahilly's stage 23) as a condensation around the joint region. In contrast, Van der Linden et al. (1987) and Burdi (1992) considered organization of the capsule to begin between weeks 9 and 11; Moffett (1957) and Sperber (1989) describe the beginning of organization in 11-week-old fetuses.

The process of joint cavitation is not synchronic since organization of the inferior joint cavity precedes that of the superior one. The inferior joint cavity begins at the end of week 9 with the appearance of small spaces or clefts between the articular disc and condyle. This differs from Perry et al. (1985), Van der Linden et al. (1987), Sperber (1989), and Ögütcen-Toller and Juniper (1993, 1994), who considered cavitation of the inferior joint cavity to begin

TABLE 3. Summary of results from other authors

	Week of development									
	6	7	8	9	10	11	12	13	14	15
Blastema temporal		d, g, j, n	a, b, e, f, i	h						
Blastema condylar		a, d, g, j, m, n	b, c, e, f, i	h						
Anlage articular disc	g	j, k, l	b, d, f							i
Anlage of the articular capsule			d	j, l	b	f, k	g		m	
Anlage of the discomalleolar ligament		g			m, n					
Condylar cartilage				j	a, b, d, k, l, m, n	c, f	g			i
Intramembranous ossification of the zygomatic process of the squamous part of the temporal bone					h, j, l					
Inferior joint cavity					b, d, h, j, k, l, m, n	a, f				
Superior joint cavity						f, j, k, m, n	b, d, h, l			

[a]Symons (1952).
[b]Moffett (1957).
[c]Baume (1962).
[d]Yuodelis (1966a).
[e]Yuodelis (1966b).
[f]Baume and Holz (1972).
[g]Moffett (1977).
[h]Perry et al. (1985).
[i]Morimoto et al. (1987).
[j]Van der Linden et al. (1987).
[k]Sperber (1989).
[l]Burdt (1992).
[m]Ögütcen-Toller and Juniper (1993).
[n]Ögütcen-Toller and Juniper (1994).

during week 10 of development. The superior joint cavity begins during week 11 of development (Van der Linden et al., 1987; Sperber, 1989; Ögütcen-Toller and Juniper, 1994). Perry et al. (1985) and Burdi (1992) considered this process as occurring during week 12 of development.

In our specimens, chondrification of the mandibular condyle was observed to begin in week 9 of development, at the same time as the inferior joint cavity appears. During week 10, the lower end of the condylar cartilage, which has a conical shape, reaches the mandibular foramen. By contrast, other studies have identified the beginning of chondrification as taking place in week 10 (Symons, 1952; Yuodelis, 1966a,b; Sperber, 1989; Ögütcen-Toller and Juniper, 1993, 1994), week 11 (Baume, 1962; Baume and Holz, 1970) and even in week 12 (Moffett, 1977). Table 3 summarizes the main results of different authors.

The influence of movement on the process of joint cavitation has been demonstrated (Murray and Drachman, 1969), and immobilization has been shown to produce an absence of joint cavities and skeletal anomalies (Sperber, 1989). Similarly, joint movement stimulates condylar chondrification (Perry et al., 1985; Sperber, 1989), and the influence of the lateral pterygoid muscle on this process has already been demonstrated (Petrovic, 1972; Strutzmann and Petrovic, 1974; Hinton, 1990; Ben-Ami et al., 1993; Takahashi, 1991; Takahashi et al., 1995). However, other studies (Glasstone, 1967, 1971; Vinkka-Puhakka and Thesleff, 1993) describe condylar cartilage development in the absence of mechanical stimulation. In our observations, during the cavitation stage, both the temporomandibular articular cavities and the condylar cartilage become organized. During this phase, buccal movements are extremely important for the organization of these structures. Moreover, recently Ranieri et al. (1996) demonstrated the existence of nerve elements in the temporomandibular region in 9- and 10-week-old fetuses. In humans, buccal movements begin during weeks 7 and 8 of development (Humphrey, 1968) at the level of the incudomalleolar joint (Mérida Velasco et al., 1990; Burdi 1992). In our opinion, the temporomandibular joint begins to play a more preponderant role than the incudomalleolar joint in buccal movements from the cavitation stage onwards.

During maturation stage we can observe insertion of the superior fascicles of the lateral pterygoid muscle into the condyle and anterointernal two-thirds of the articular disc, whereas the anteroexternal third at the articular disc is associated with the temporal and masseter muscles (Mérida Velasco et al., 1993).

During week 13 of development we observed invagination of vascular mesenchyme in the external portion of the condylar cartilage. These formations were described by Vinogradoff (1910), who called them "crampons." During week 16 of development we observed the vascular canals as clearly evident. By contrast, Symons (1952) found that the vascular canals of the condylar cartilage appeared in 19-week-old specimens, whereas Blackwood (1965) described them during week 15. Moreover, Blackwood (1965) and Wright and Moffett (1974) postulated that the function of this vascularization is to provide nutrition for the cartilage, enabling the mandible to grow more quickly in order to make room for the growth and eruption of the deciduous teeth. Thilander et al. (1976) reported a decrease in the cartilage's vascular canals from the age of 5 to

6 years onwards, whereas Takenoshita (1987) reported these to progressively decrease after 10 years.

The posterior portion of the joint capsule inserts into the squamous part of the temporal bone, the tympanic bone and in the posterior surface of the condyle. The discomalleolar ligament is located between the capsular insertion and the squamous part of the temporal bone and tympanic bone. Studies by Smeele (1988) revealed that the superior and inferior lamellae of the capsule demarcate both cavities dorsally, and an intermediate lamina which corresponds to the discomalleolar ligament takes insertion in the tympanic bone. Smeele (1988) named this arrangement during the fetal period the trilaminar region. Nevertheless, in adults the posterior portion of the capsule (Rees, 1954) was shown to be constituted by two laminae: an upper lamina reinforced medially by the discomalleolar ligament, inserting in the squamous part of the temporal bone and tympanic bone, and a lower lamina that was attached to the posterior surface of the condyle (Mérida Velasco et al., 1997; Rodríguez Vázquez et al., 1998).

The posterior joint region is associated with the still wide tympanosquamosal fissure through which the chorda tympani nerve, Meckel's cartilage, the gonial bone, the discomalleolar ligament and branches of the anterior tympanic vessels proceed (Rodriguez Vázquez et al., 1992, 1993; Mérida Velasco et al., 1997a). More specifically, development of the discomalleolar ligament begins in week 8 of development (O'Rahilly's stage 23), starting from a band of mesenchyme that extends from the condyle to the lateral surface of Meckel's cartilage. A similar arrangement was described by Smeele (1990). However, Ögütcen-Toller (1995) described the discomalleolar ligament as appearing during week 10 as a band of mesenchyme 150 µm thick.

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