A novel system for classifying tooth root phenotypes

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Abstract

Human root and canal number and morphology are highly variable, and internal root canal form and count does not necessarily co-vary directly with external morphology. While several typologies and classifications have been developed to address individual components of teeth, there is a need for a comprehensive system, that captures internal and external root features across all teeth. Using CT scans, the external and internal root morphologies of a global sample of humans are analysed (n=945). From this analysis a method of classification that captures external and internal root morphology in a way that is intuitive, reproducible, and defines the human phenotypic set is developed. Results provide a robust definition of modern human tooth root phenotypic diversity. Our method is modular in nature, allowing for incorporation of past and future classification systems. Additionally, it provides a basis for analysing hominin root morphology in evolutionary, ecological, genetic, and developmental contexts.

Introduction

Human dental morphology is a diverse collection of non-metric traits: cusp numbers, fissure and ridge patterns, root number and shape, and even congenital absence. Recording systems, such as the widely utilized Arizona State University Dental Anthropology System (ASUDAS) [1,2], have been developed to catalogue these traits and their variants under a standardized scoring procedure; and to study how these variants are partitioned within and between populations. However, dental trait scoring systems are overwhelmingly focused on tooth crown morphology, with less attention paid to roots. Like tooth crowns, roots exhibit considerable variability in number, morphology, and size. For example, premolars have been reported as having between one to three roots [3,4], while maxillary and mandibular molars have between one and five roots [5–8]. The literature has also long recognized several unusual morphological variants such as Tomes' root [9], taurodont roots [10], and C-shaped roots [11]. Additionally, the diversity of the canal system, both in number and configuration, has been an area of extensive study (Table 1).

As the number of catalogued external and internal morphologies grow, there is an increasing need for a comprehensive system, that can be used for documented and new morphotypes, and is robustly capable of describing the total human tooth root phenotype. The aim of this study is to 1) systematically describe the diverse internal and external morphologies of the human tooth root complex (i.e., all roots present in an individual tooth); and 2) define, develop, and provide a comprehensive system that captures these morphologies in all the teeth of both jaws for analysis.

Background

The studies discussed below have addressed root number, canal number, external root morphology, canal morphology, and canal configuration independently. However, they comprise only parts of the tooth root complex, and thus provide a basis for a comprehensive phenotype system.

Root number

Root number is probably the best studied element of root morphology, as counting roots is easily accomplished in extracted and in-situ teeth. Early studies of roots were primarily descriptive of root number, and the occasional metrical analysis [12,13,22–26,14–21]. Maxillary premolars are reported as having the most variation in number of roots, with a higher percentage of P^3s having two roots (or at least bifurcated apices), while P^4 is typified by one root. Three rooted maxillary premolars (P^3 and P^4) have been documented in modern humans [4,17,18,20,27,28] but are extremely rare. Scott and Turner [2] report a world frequency of 4.9-65% for two-rooted premolars. Their results show that Sub-Saharan Africans have the highest frequency at 65%, 40% in West Eurasian populations, 20-30% in East Asian populations, and 5-15% in Northeast Siberians and Native Americans. In contrast to the maxilla, the most frequent form of mandibular P_3s and P_4s is single rooted; though P_3s are occasionally two-rooted or, more rarely, thee rooted [29–31].

Maxillary molars are generally three rooted; though molars with two, four [32,33] and five [34] roots have been reported. Variation in root number has been recorded for three rooted M^2s; with Australian Aboriginals having the highest reported percentage at 95.8% [15]. Sub-Saharan Africans also have a high frequency of three-rooted M^2s at 85%, Western Eurasians and East Asians ranging from 50-70% and American Arctic populations ranging from 35-40% [2]. Three European samples by Fabian, Hjelmmanm, and Visser (in [24]) report an average of 56.6%, in accordance with Scott and Turner [2]. Inuit populations are lower with East Greenland populations at 23.7% [22] and 30.7-31.3% in two prehistoric Alaskan populations [35].

Unlike their maxillary counterparts, mandibular molars are less variable in root number. A rare exception, mandibular molars sometimes exhibit a third accessory root (Fig 1). They are generally smaller than the mesial and distal roots of the mandibular molars, and most frequently appear in lower first molar. In the ASUDAS these are referred to as three rooted molars [35]. The clinical literature applies a different typology and identifies several variants. These include – (1) The radix entomolaris (En) accessory root arising from the lingual surface of the distal root; (2) the radix paramolaris (Pa) arising from buccal side of the distal root; and (3), furcation root (Fu) projecting from the point of bifurcation between roots [36].

Fig 1. **Examples of accessory roots.** Mandibular molars with A1 and A2: radix entomolaris (left=distolingual surface, right = lingual surface), B: M_3 with radix entomolaris (lingual view), C: M_1 with furcation root (buccal view), D: M_1 with fused radix paramolaris (buccal view). Modified from Calbersen et al., [36].

The entomolaris trait is expressed with high frequency (20-25%) in Sino-American populations (East Asia, North East Siberia, American artic), with one Aleut population exhibiting a sample frequency of 50% [2,37]. The trait also appears in 15.6% of North American Athabascans and Algonquin Native American tribes [38]. Tratman [19] claimed the trait showed a distinct dichotomy between European and Asian populations, as did Pedersen [22]. Comparatively, this trait appears in less than 1% of populations from Sub-Saharan Africa, West Eurasia, and New Guinea (ibid). The trait has been reported in extinct hominins [39], but see Scott et al., [40] for a further discussion.

Single rooted molars usually appear in three forms: C-shaped M_2s, taurodont M_1s-M_3s, and pegged M^3s/M_3s (Fig 2, A-C). C-shaped molars are common in Chinese populations with a frequency as high as 40% [41]. The trait has a low frequency of 0-10% in Sub-Saharan Africans [42], 1.7% in Australian Aboriginals [15], and 4.4% in the Bantu (Shaw, 1931). Rare in modern humans, taurodont molars occur when the root trunk and internal pulp cavity are enlarged and apically displaced. This form was first classified by Keith [10] in *Homo neanderthalensis*. Externally, taurodont roots are cylindrical in shape (Fig 2B). While sometimes confused with C-shaped molars, taurodont roots lack an internal and external

180° arc, and are instead circular in cross-section, usually with a bifid apical third. Pegged third molars are the most variable in size and morphology [35]. Their reduction has a genetic component and patterned geographical variation [35,43]. Pegged third molar roots are associated with a reduced crown, appear more frequently in the maxilla than the mandible, and are circular in cross-section

Multi-rooted anterior teeth are exceptionally rare [44]. Alexandersen [45] compiled data on double rooted mandibular canines from several European countries, two Danish Neolithic samples, and two medieval samples; in which they attain a frequency of 4.9 -10%. His findings suggest that the double rooted canine trait is a European marker. However, Lee and Scott [46] found the variant in 1-4% of an East Asian population sample (Central Plains China, Western China and Mongolia, Northern China, Ordos Region, and Southern China). The authors interpreted this as possible evidence of an eastward migration of Indo-European speaking groups into China and Mongolia.

Fig 2. **Unusual root forms.** A. C-shaped tooth in (clockwise from top left) lingual, cross-section at the cemento-enamel junction, cervical third, middle third, apical third, and apical views. B. Taurodont molar, apically displaced pulp chamber and canals outlined in white. C. Peg-shaped root. Images A, C from the Root Canal Anatomy Project http://rootcanalanatomy.blogspot.com/ (accessed 10 March 2021). Image B from http://www.dentagama.com (accessed 27th March 2021).

External Root morphology

Studies of root morphologies in cross-section have recognised forms such as 'plate-like' and 'dumb-bell', in the mandibular molars of humans, great apes, cercopithecoids, and Plio-Pleistocene hominins [47–50]; while cross sections of australopith anterior teeth have been described as 'ovoid' [51]. Though these descriptions appear from time to time in the literature, they are inconsistently applied, have not been described in detail required for comparative studies, or codified into a classification system which can be consistently applied.

Some exceptions exist. Tomes' roots [9] have a long history of study in the anthropological literature, and are included in the ASUDAS. These single rooted teeth are part of a morphological continuum in which the mesial surface of the root displays, in varying degrees of depth, a prominent developmental groove [1]. Tomes first described this root configuration in modern human mandibular premolars and classified it as a deviation from the "normal" European single rooted premolar (ibid). Tomes' root appears in 10% of P_3s and P_4s of the Pecos Native American Tribe [18], 36.9% of P_3s and 8.4% for P_4s in the Bantu [17], and >25% for Sub-Saharan African groups [2]. In contrast, P_3 Tomes' roots account for 0-10% of Western Eurasian populations and 10-15% of North and East Asian population (ibid). In its most extreme form, the groove appears on mesial and distal surface, and can result in bifurcation of the root. In cross section, Tomes' roots have a V-shaped 'notch' where the two radicals are dividing. Occasionally, this division results in bifid apices or two separate roots, depending on the level of bifurcation [52].

Another unusual morphology, the C-shaped molar (Fig 2A) consists of a single root in an 180° arc, with a buccally oriented convex edge, and are most common in the 2nd mandibular molar [8,41]. In certain cases, two mandibular molar roots are fused on their buccal side giving them the appearance of C-shaped molars; however, the two forms are not homologous and can be discerned by the former's lack of a uniform, convex external buccal surface, and C-shaped canal.

Occasionally two roots can become fused (Fig 3). The reasons for fusion are unclear, but may be due to suppression or incomplete fusion of the developing tooth root's interradicular processes during root formation [53,54]. Fused roots can be joined by dentine, have linked pulp chambers and/or canals [55]. In such a scenario adjacent root structures are apparent, but their separation is incomplete. Fused roots are most common in the post-canine tooth row of the maxillary arch.

Fig 3. **Fusion of multiple roots into right single roots in maxillary 2nd molars.** A. fused mesial E and distal G root types. B. fused mesial E and distal H root types. C. fused lingual G and distal P root types. Images A, B, and C from the Root Canal Anatomy Project https://rootcanalanatomy.blogspot.com/ (accessed 10 March 2020).

Root canals

In its simplest form, a root canal resembles a tapered cylinder, extending from the pulp chamber beneath the crown, and exiting the root apex. Often, individual canals are circular or ovoid in cross section, even when multiple canals appear in the same root (Fig 4).

Fig 4. **Canal morphologies in cross section.** Left to right: Round and ovoid canal forms. Gray is canal shape, black is external form of the tooth root.

With exception of the anterior teeth, this is rarely the case, and there are often multiple canal configurations within a single root (Fig 5). A wide range of canal configurations have been reported [11,56–58], though the number of configurations vary by study. Often, these discrepancies are due to the inclusion or exclusion of accessory canals (lateral and furcation canals), which branch from the main canal structure, like the roots of a tree, at the point of bifurcation or the apical third. However, most practitioners opt to exclude these from typologies as they are not continuous structures from the pulp chamber to the root apex.

Fig 5. **Vertucci's widely used canal classification system.** Root and canal number do not always conform to one another. Black area represents pulp chambers and various canal configurations [56].

In conjunction with external form, canal morphology has proven useful for hominin classification [59–62]. In mandibular premolars, researchers have shown that combined external morphologies and canal configurations can differentiate robust and gracile australopiths [61,63,64]. However, it is unclear how internal variation relates to external morphology or is partitioned between and across populations.

Canal classification systems

The most widely used canal typology system contains eight types (Fig 5), which can, theoretically, be found in any tooth in the jaws [56]. However, this classification system does not include all known canal types. For example, canal isthmuses - complete or incomplete connections between two round canals are frequently found in molars (Fig 6, left), though they appear in other roots [58]. These canal configurations are distinct from those described by Vertucci et al., [56] . Likewise, C-shaped canals have been the subject of several studies [8,65,66], and their configurations are nearly identical (though ordered differently) to the canal isthmuses described by Hsu and Kim [58], only stretched around an 180° arc (Fig 6, right). These same isthmus canal configurations can also be found in Tomes' roots [67,68].

Fig 6. **Two different classification methods for canal isthmuses.** Left: Canal isthmuses, modified from Hsu and Kim [58]. Right: C-shaped root canals, modified from Fan et al., [11].

Many classification systems have been introduced (Table 1). However, they often focus on one tooth type or morphology. Of the 27 traits catalogued by the ASUDAS, only root number for specific teeth (P^3, M^2, C_1, M_1, and M_2) and external morphology (Tomes' root) are included [1]. Others systems are only focused on the canal configurations of maxillary premolars [33], the mesial canals of mandibular 1st and 2nd molars [69], or more narrowly, unusual canal types such as isthmus [58] or C-shaped canals [11,66]. Others propose separate classificatory nomenclature based on root number[57], or maxillary [70] and mandibular molars [71].

Table 1. Previous typological studies of tooth roots and canals in modern humans.

Authors	Technique	Roots	Canals	Teeth
Tomes [9]	Direct observation	Yes	-	Premolars
Keith [10]	Direct observation	Yes	Yes	Molars
Ackerman et al.,[72]	Radiography	Yes	Yes	Molars
Vertucci et al., [56]	Direct observation using dye	-	Yes	Maxillary premolars
Abbot [73]	Direct observation, radiography	Yes	Yes	All teeth, focus on premolars
Turner et al., [1]	Direct observation	Yes	-	All
Carlsen and Alexandersen [74]	Direct observation	Yes	-	Mandibular molars
Hsu and Kim [58]	Sectioning of tooth, direct observation using dye	-	Yes	Maxillary and mandibular pre- and first molars.
Fan et al., [11]	Radiography	Yes	Yes	2nd mandibular molar
Moore et al., [61]	CT	Yes	Yes	Premolars
Ahmed et al., [57]	micro CT	-	Yes	All

While canal number and morphology do not always conform to external number and morphology [50,55,61], the literature on the relationship between internal and external morphologies is sometimes inconsistent. For example, Vertucci *et al.* [56] categorize maxillary premolars with two separate canals as type IV (Fig 6). However, it is unclear if this classification is to be applied only to two canals encased in a single or two-rooted tooth. Canal shape can also change over time due to dentin deposition [75]. While some variation may be due to age and/or biomechanical factors, there is currently no methodology to classify these changes.

Materials and Methods

CT scans

Using cone-beam computed tomography (CBCT or CT), we analysed both sides of the maxillary and mandibular dental arcades of individuals (n= 945) from osteological collections housed at the Smithsonian National Museum of Natural History (SI), American Museum of Natural History (AMNH), and the Duckworth Collection (DC) at the University of Cambridge Leverhulme Centre for Human Evolutionary Studies. Full skulls of specimens from the SI and AMNH were scanned by Dr. Lynn Copes [76] using a Siemens Somatom spiral scanner (70 μA, 110 kV, slice thickness 1.0 mm, reconstruction 0.5 mm, voxel size mm^3: 1.0x1.0x0.3676). Full skulls of specimens from the DC were scanned by Professor Marta Miraźon-Lahr and Dr. Frances Rivera [77] using a Siemens Somatom Definition Flash scanner at Addenbrooke's Hospital, Cambridge England (80μA, 120kV, slice thickness 0.6mm, voxel size mm^3: 0.3906x0.3906x0.3). For all collections, crania and mandibles were oriented on the rotation stage, with the coronal plane orthogonal to the x-ray source and detector. Permission to use the scans has been granted by Dr. Copes, Professor Miraźon-Lahr and Dr. Rivera. A complete list and description of individuals included in this study is listed in the S1 table.

Transverse CT cross sections of roots and canals were assessed in the coronal, axial, and sagittal planes across the CT stack, using measurement tools in the Horos Project Dicom Viewer (Fig 7) version 3.5.5 [78]. Only permanent teeth with completely developed roots and closed root apices were used for this study. While information for all teeth from both sides of the maxillary and mandibular arcades was recorded, only the right sides were used to avoid issues with asymmetry and artificially inflated sample size.

Fig 7. **Horos Dicom Viewer 2D orthogonal view used to assess root and canal morphologies.** Left: Coronal view at mid-point of roots. Centre: Anterior view at midpoint of roots. Right: Lateral view at midpoint of roots

External root morphology

External root morphology was assessed at the measured mid-point of the root, bounded by the cemento-enamel junction (CEJ) and root apex/apices. The midpoint was chosen as a point of inspection because (a) the root has extended far enough from the CEJ, and in the case of multi-rooted teeth, from the neighboring roots to be structurally and developmentally distinct [79]; and (b) at a point in the eruptive phase in which the adjoined tooth crown is in functional occlusion [80]; and, (c) does not reflect the morphological alteration common to the penetrative phase in which the apical third of the root becomes roughened and/or suffers ankylosis or concrescence due to penetration of the bones of the jaws [80].

Root and canal number

To determine root and canal number, we apply the Turner Index [1], which compares the point of bifurcation (POB) relative to total root or canal length. When this ratio is greater than 33% of the total root or canal length, the root or canal is classified as multi-rooted. When the ratio is less than 33% the root or canal is considered single rooted, or with a bifid apical third (Fig 8). Here, we define a single root canal as a canal which extends from the pulp chamber within the crown and exits at a single foramen. We do not include accessory canals in our study.

Fig 8. **Determination of root and canal number.** Left = Distal view of single-rooted premolar with bifurcation of the apical third of the root. Middle: Lingual view of double-rooted mandibular molar. Right: Distal root of double-rooted mandibular molar with examples of canal counts in solid gray. Dotted gray lines indicate canal/s position in root. CEJ = Cemento-enamel junction, POB = Point of bifurcation, Solid gray = canals. CT = cervical third, MT = middle third, AT = apical third.

Canal morphology and configuration

Individual canals are circular or ovoid in cross section. Here we classify circular, or round canals as R, and ovoid canals as O. These are appended numerically to reflect the number of canals present. For example, R2 simply describes two, distinct circular canals, while O describes a single ovoid canal (Fig 9).

Fig 9. **Canal morphologies in cross section.** Gray is canal shape, black is external form of the tooth root.

To classify canal configurations, we have simplified canal configurations into five categories, R-R5, that reflect canal number and account for fusion/division of canals (Fig 10). These categories can be found in any tooth and are applied to single roots within the root complex (e.g., 3 roots, each with a single canal, would not be designated R3, but R for each canal per root).

Fig 10. **Canal counts and degrees of separation.** Solid grey = root canal forms. CT = cervical third, MT = middle third, AT = apical third.

Because C-shaped canal configurations [11] are nearly identical to the canal isthmuses described by Hsu and Kim [58] (Fig 6), we combined and simplified both isthmus and C-shaped canal systems into one (Fig 11). We describe five categories for canal isthmuses. Here, i1 is defined as a single root with two unconnected canals (here classified as R2, Figs 9 & 10); i2 is defined as a complete connection between separate canals; i3 is defined by one or both canals extending into the isthmus area, but without complete connection; i4 is defined by an incomplete connection between three (sometimes incomplete) canals; and i5 is defined as a thin or sparse connection between two canals. These same isthmus canal configurations can also be found in Tomes' roots.

Fig 11. **Combined isthmus classification system.** Based on systems developed by Hsu and Kim [58] and Fan et al. [11]. Black is external root form and grey is canal form. P = plate-shaped, Cs = C-shaped, and T = Tomes' root.

Anatomical descriptions

Categorically, incisors are indicated by an I, canines a C, premolars with P, and molars use M. Tooth numbers are labelled with super- and subscripts to differentiate the teeth of the maxilla and mandible. For example, M^1 indicates the 1st maxillary molar while M_1 indicates the 1st mandibular molar. Numerically, incisors are numbered either 1 or 2 for central and lateral incisors respectively. Canines are marked 1 as there exists only one canine in each quadrant of the jaws. Through the course of evolution, apes and old world monkeys have lost the first and second premolars of their evolutionary ancestors, thus the remaining 2 premolars are numbered 3 and 4 [81,82].

Unlike the anatomical surfaces and directions used for tooth crowns, there exists no formula for tooth roots. However, classical anatomical terms – mesial, buccal, distal, lingual, or combinations of (e.g., mesio-buccal), can be used to describe the location of roots and canals. Additionally, we use the term axial to describe a single or centrally located canal within a single-rooted tooth. Because anatomical location rather than anatomical surface is being employed, buccal replaces labial (for anterior teeth) when describing roots.

Results

We analysed CT scans of 5,970 teeth (Table 2) of 945 individuals from a global sample (supplementary material) to identify morphologies which are useful for classifying the tooth root complex of modern human teeth. We first present descriptive statistics of external and internal morphologies found in our sample. We then define and present a novel tooth root classification system comprised of phenotype elements, each of which describes a property of the individual roots, and the root complex as a whole. Each element (E) within the set provides information on root (E1) and canal (E2) number; identification and location of roots and canals in the root complex (E3); external root form (E4); and (E5) internal canal forms and configurations. Combined elements (for example root number and internal canal form combined together) can be treated as phenotypes or separated and analysed by their constituent parts. The system, described below, allows us to define a finite set of possible root phenotypes and their permutations (the realized phenotypic set) and analyse diversity in a constrained morphospace.

Table 2: Tooth counts of the right side of the maxillary and mandibular dental arcades.

Tooth	**n**	**Tooth**	**n**	**Total**
Maxilla		Mandible		
I^1	204	I_1	204	408
I^2 I^2 CON	248 1	I_2 I^2 CON	247 1	495 -
C^1	406	C_1	295	701
P^3	515	P_3	343	858
P^4	467	P_4	313	780
M^1	697	M_1	410	1,107
M^2	596	M_2	385	981
M^3 M^3 CON	362 28	M_3 M^3 CON	278 25	640 -
Total	3,495	-	2,475	5,970

Superscript = maxilla, subscript = mandible. I = incisor, C = canine, P = premolar, M = molar. CON = congenitally absent teeth (discussed in section 1.5).

Root number

In aggregate, the number of roots in teeth from our sample are between one and four (Table 3). Anterior teeth almost always having a single root, the exception being two mandibular canines, premolars between one and three roots, and molars between one and four roots. Entomolaris, or three-rooted molars, appear in 18.05 % M_1s, 1.23% of M_2s, and 5.94% of M_3s, while paramolaris appears in 3.63% of M_3s.

Table 3: Number of roots in teeth of the maxilla and mandible by tooth

Tooth	Root number	n	Total Roots	% of teeth*	Tooth	Root number	n	Total Roots	% of teeth*
Maxilla					Mandible				
I^1	1	204	204	100.00	I_1	1	204	204	100.00
I^2	1	248	248	100.00	I_2	1	247	247	100.00
C^1	1	406	406	100.00	C_1	1	293	297	99.32
						2	2		0.68
P^3	1	295	739	57.28	P_3	1	341	345	99.42
	2	216		41.94		2	2		0.58
	3	4		0.78					
P^4	1	405	530	86.72	P_4	1	313	313	100.0
	2	61		13.06					
	3	1		0.22					
M^1	1	2	2,060	0.29	M_1	2	336	894	81.95
	2	28		4.02		3En	74		18.05
	3	666		95.55					
	4	1		0.14					
M^2	1	56	1,561	9.39	M_2	1	49	727	12.73
	2	117		19.63		2	330		85.71
	3	421		70.64		3	1		0.26
	4	2		0.34		3En	5		1.30
M^3	1	89	831	24.59	M_3	1	20	563	7.19
	2	82		22.65		2	231		83.09
	3	186		51.38		3En	16		5.76
	4	5		1.38		3Pa	11		3.96

* From Table 2. Congenitally absent teeth not included in statistics for this table.
En = Entomolaris, Pa = Paramolaris.

Canal number

Teeth in our study contain between one and six canals (Table 4), and it is not uncommon for a single root to contain two or more canals, especially in the molars. With the exception of I^1, all single rooted anterior teeth have a double canaled variant. Molars have the most canals per tooth, with M^1s showing the most variation. With the exception of I^1, canal number exceeds root number (Table 3).

Table 4: Number of canals per tooth in the maxilla and mandible by tooth

Tooth	Canal number	n	Total Canals	% of teeth*	Tooth	Canal number	n	Total Canals	% of teeth*
Maxilla					Mandible				
I^1	1	204	204	100.00	I_1	1	180	228	88.24
						2	24		11.76
I^2	1	247	249	99.60	I_2	1	208	286	84.21
	2	1		0.40		2	39		15.79
C^1	1	405	407	99.75	C_1	1	273	317	92.54
	2	1		0.25		2	22		7.46
P^3	1	82	959	15.92	P_3	1	254	435	74.05
	2	422		81.94		2	86		25.07
	3	11		2.14		3	3		0.87
P^4	1	233	708	49.89	P_4	1	300	326	95.85
	2	228		48.82		2	13		4.15
	3	5		1.07					
	4	1		0.22					
M^1	2	4	2,431	0.57	M_1	2	27	1,431	6.59
	3	355		50.93		3	167		40.73
	4	333		47.78		4	205		50.00
	5	4		0.57		5	10		2.44
	6	1		0.14		6	1		0.24
M^2	1	8	1,910	1.34	M_2	1	2	1,107	0.52
	2	21		3.52		2	93		24.16
	3	408		68.46		3	241		62.60
	4	159		26.68		4	49		12.73
M^3	1	32	1,065	8.84	M_3	1	10	748	3.60
	2	24		6.63		2	86		30.94
	3	239		66.02		3	162		58.27
	4	67		18.51		4	20		7.19

* From Table 2. Congenitally absent teeth not included in statistics for this table.

Anatomical orientation of canals in the root complex

The majority of teeth follow a similar anatomical pattern of having axially (A) oriented, buccal (B) and lingually (L) oriented, or mesially (M), distally (D), and lingually (L) oriented canals and roots. Other orientations, for example MB1DB1ML1DL1R, are relatively rare, and only appear in molars. In cases where there are multiple canals appear in a single root these are almost always found in the mesial or buccal orientations (e.g., M2D1L1, B2L1).

Table 5: Anatomical orientation of the canals in the maxilla and mandible by tooth

Tooth	External morphology	n	% of teeth*	Tooth	External morphology	n	% of teeth*
	Maxilla				Mandible		
I^1	A	204	100.00	I_1	A	180	88.24
					B1L1	24	11.76
I^2	A	247	99.60	I_2	A	208	84.21
	B1L1	1	0.40		B1L1	39	15.79
C^1	A	405	99.75	C_1	A	273	92.54
	B1L1	1	0.25		B1L1	22	7.46
P^3	A	82	15.92	P_3	A	254	74.05
	B1L1	421	81.75		B1L1	86	25.07
	B1L2	1	0.19		M1D1L1	3	0.87
	B2L1	6	1.17				
	M1D1	1	0.19				
	M1D1L1	4	0.78				
P^4	A	233	49.89	P_4	A	300	95.85
	B1L1	228	48.82		B1L1	13	4.15
	B2L1	3	0.65				
	B2L2	1	0.21				
	M1D1L1	2	0.43				
M^1	B1L1	3	0.43	M_1	M1D1	27	6.59
	M1D1	1	0.14		M1D1L1	12	2.93
	M1D1L1	354	50.80		M2D1	156	38.05
	M1D1L2	2	0.29		M2D1L1	59	14.39
	M1D2	1	0.14		M2D2	144	35.12
	M1D2L1	1	0.14		M2D2L1	3	0.73
	M1L1	1	0.14		M2D3	5	1.22
	M2D1	1	0.14		M3D1	1	0.24
	M2D1L1	327	47.07		M3D2	2	0.49
	M2D1L2	2	0.29		M3D3	1	0.24
	M2D2L1	1	0.14				
	M2D2L2	1	0.14				
	M3D1L1	1	0.14				
	MB1DB1ML1DL1	1	0.14				
M^2	A	8	1.34	M_2	A	2	
	B1L1	20	3.36		B1D1L1	1	
	M1B1D1L1	1	0.17		B2L1	2	
	M1D1	1	0.17		B2L2	1	
	M1D1L1	408	68.46		M1B1D1	7	
	M1D2L1	2	0.33		M1D1	93	
	M2D1L1	153	25.67		M1D1L1	1	
	MB1DB1ML1DL11	2	0.33		M1D2	1	
	ML3D1	1	0.17		M2D1	229	
					M2D1L1	4	
					M2D2	42	
					M3D1	2	
M^3	A	32	8.84	M_3	A	10	
	B1L1	17	4.70		B2L1	1	
	B2D1L1	1	0.28		M1B1D1	8	
	M1B1D1L1	2	0.55		M1B2D1	1	

M1D1	7	1.93	M1D1	84
M1D1L1	235	64.92	M1D1L1	9
M1D1L2	1	0.28	M2B1D1	2
M1D2	3	0.83	M2D1	147
M1D2L1	1	0.28	M2D1L1	9
M2D1	1	0.28	M2D2	6
M2D1L1	45	12.43	M3D1	1
M2D2	11	3.04		
MB1DB1ML1DL1R	5	1.38		
ML3D1	1	0.28		

* From Table 2. Congenitally absent teeth not included in statistics for this table. A = axial, M = mesial, B = Buccal, D = Distal, L = Lingual.

External root morphology at midpoint

Similar to the variation found in tooth cusp morphology [1], external root morphologies exist as distinctive, yet easily recognizable anatomical variants (Fig 12). While these morphologies frequently extend through the apical third to the apex of the root, occasionally they are bifid (Bi), and we have noted this where applicable.

Fig 12. **External root morphologies.** Left and right columns = axial CT slices showing external root morphologies at the middle third (MT) and apical third (AT). Centre illustrations = root morphologies at centre of root/s.

Though some of these morphologies have been discussed in the literature, their descriptions are inconsistent (e.g., hourglass, plate). Table 6 includes definitions and descriptions of the root morphologies shown in Fig 12. Two of the morphologies, wedge (W) and kidney (K), are described here for the first time.

Table 6: Description of external tooth root morphologies at the midpoint

Morphology	Description	Reference
Globular (G)	Round or circular in shape. While this form varies greatly in size, it is relatively invariant in shape, and in that all edges are relatively equidistant from the center.	[83]
Elliptical (E)	While size, and distance of the edges from the center vary, elliptical shaped roots are distinct from others in that they look like a squashed circle. Sometimes these forms are perfectly symmetrical and other times they resemble and egg. However, a consistent feature are there continuously smooth edges which are concentric to the canals.	[61,80,83]
Wedge (W)	Wedge shaped roots are easily distinguished by their 'tapered' appearance. Sometimes these forms take the shape of a triangle with three edges and corners, while other times	This study

	they appear more teardrop shaped with a slight constriction in the middle. However, they are easily distinguished as the buccal end is always noticeably wider than the lingual end.	
Hourglass (H)	Hourglass shaped roots have often been confused with plate-shaped roots, or occasionally, elliptical roots. However, this form is distinct and easily identified by its bulbous ends and constricted center. This constriction can be so pronounced that the root appears almost as a lemniscate in cross-section.	This study, but see [47–49] for complimentary and contradictory definitions.
Kidney (K)	Kidney shaped roots are defined by their opposite convex and concave sides. Sometimes these curvatures are pronounced, and other times they are more subtle. However, these two features are always apparent, and distinct from other forms.	This study
Plate (P)	Plate shape roots are similar to hourglass and elliptical roots in their dimensions but are easily distinguished by their flat edges. In some variants the corners are rounded, while in others they are square.	This study, but see [47–49] for complimentary and contradictory definitions.
Tomes' (T)	Tomes' roots have been documented for nearly a century and appear in a number of classification systems including the ASUDAS. They are single rooted teeth that appear to be 'splitting' into two roots. In cross section they sometimes look like c-shaped molar roots. However, one of their distinguishing features is that they are only found in mandibular premolars.	[1,9]
C-shaped (CS)	C-shape molars are primarily found in the second molars of the mandible, though they rarely appear in the first and third mandibular molars as well. There is a substantial clinical literature covering their distinct morphology and prevalence. Unlike Tomes' roots they do not appear to be splitting into two roots. Rather, they are a single, continuous root structure. Like kidney shaped roots they have opposite convex and concave sides. However, their curvature is more pronounced, in nearly a 180° arc with ends that are parallel to one another.	[8,11,84]

External root morphologies appear in different frequencies in each tooth, and some morphologies do not appear in some teeth at all (Table 7). The number of morphologies increase posteriorly along the tooth row, and M_1s have the most morphologies. Part of this is due to the number of bifid (Bi) variants (e.g., EBi, PBi, etc.), as well as the presence of pegged and fused roots (Tables 8 and 9, respectively).

Table 7: Number of external root morphologies in the maxilla and mandible by tooth

Tooth	**External morphology**	**n**	**% of roots***	**Tooth**	**External morphology**	**n**	**% of roots***
Maxilla				Mandible			
I^1	E	69	33.82	I_1	E	13	6.37
	G	117	57.35		G	1	0.49
	P	8	3.92		K	3	1.47
	W	10	4.91		P	177	86.76
					W	10	4.90

I^2	E G P W	120 25 97 6	48.39 10.08 39.11 2.42	I_2	E H K P W	7 1 10 219 10	2.83 0.40 4.05 88.66 4.05
C^1	E EBi† G P W	149 1 4 135 117	36.70 0.25 0.99 33.25 28.83	C_1	E G H K P W WBi	54 6 6 2 141 87 1	18.18 2.02 2.02 0.67 47.47 29.29 0.34
P^3	E G H HBi K KBi P PBi W	10 402 80 40 38 5 143 12 9	1.35 54.40 10.83 5.41 5.14 0.68 19.35 1.62 1.22	P_3	E G H K P T TBi W	62 14 1 3 145 75 8 37	17.97 4.06 0.29 0.87 42.03 21.74 2.32 10.72
P^4	E G H HBi K KBi P PBi W	24 106 70 21 31 3 266 4 4	4.53 20.00 13.21 3.96 5.85 0.57 50.19 0.75 0.75	P_4	E G HBi K P T TBi W	122 21 1 1 155 9 1 3	38.98 6.71 0.32 0.32 49.52 2.88 0.32 0.96
M^1	E G H K P PBi W WBi	500 266 11 49 668 4 536 2	24.27 12.91 0.53 2.38 32.43 0.19 26.02 0.09	M_1	E G H HBi K KBi P PBi W	20 76 188 61 73 4 437 17 18	2.24 8.50 21.03 6.82 8.17 0.45 48.88 1.90 2.01
M^2	E G H HBi K KBi P W	451 371 9 2 80 1 262 241	28.89 23.76 0.58 0.13 5.12 0.06 16.78 15.43	M_2	CS CSBi E G H HBi K KBi P PBi W	33 1 33 15 143 17 206 4 256 5 1	4.54 0.14 4.54 2.06 19.67 2.34 28.34 0.55 35.21 0.69 0.14
M^3	E	105	12.64	M_3	CS	6	1.07

	G	338	40.67		E	75	13.32
	H	12	1.44		G	72	12.79
	HBi	5	0.60		H	49	8.70
	K	41	4.93		HBi	4	0.71
	P	115	13.84		K	182	32.33
	PBi	5	0.60		KBi	3	0.53
	W	103	12.39		P	155	27.53
					PBi	2	0.36
					W	4	0.71

* from Table 3, **Bi** = bifid. Congenitally absent teeth not included in statistics for this table.

Pegged (Mi) roots while globular in cross section, are their considered their own distinct morphology as they are a form of microdontia [85]. They are relatively rare in our sample and only appear in M^3 and M_3 (Table 8).

Table 8: Type and number of teeth with pegged roots

Tooth	**External morphology**	**n**	**% of roots***	**Tooth**	**External morphology**	**n**	**% of roots***
Maxilla				Mandible			
M^3	Mi	5	0.60	M_3	Mi	6	1.07

* from Table 3

Fused roots are almost always found in the molars and are more common in the maxillary molars (Table 9). In almost all cases fusion includes the mesial (M) root, and it is not uncommon for fused roots to have some degree of bifurcation (Bi).

Table 9: Type and number of roots showing fusion morphologies

Tooth	**External morphology**	**n**	**% of roots***	**Tooth**	**External morphology**	**n**	**% of roots***
Maxilla				Mandible			
P^4	MLFBi	1	0.19	M_2	MDF	13	1.79
M^1	MDF	4	0.19	M_3	MDF	5	0.89
	MLF	1	0.05				
	MLFBi	3	0.15				
	DLF	8	0.39				
	DLFBi	8	0.39				
M^2	BLF	3	0.19				
	DLF	8	0.51				
	DLFBi	2	0.13				
	MDF	12	0.77				
	MDFDLF	4	0.26				
	MDFMLF	2	0.13				
	MDFMLFBi	1	0.06				
	MLF	60	3.84				
	MLFBi	21	1.35				

	MLFBiDLF	1	0.06				
	MLFBiMDF	1	0.06				
	MLFDLF	23	1.47				
	MLFDLFBi	3	0.19				
	MLFMDF	4	0.26				
M^3	DLF	15	1.81				
	MDF	14	1.68				
	MDFDLF	1	0.12				
	MLF	25	3.01				
	MLFBi	8	0.96				
	MLFBiDLF	2	0.24				
	MLFDLF	36	4.33				
	MLFMDF	1	0.12				

* from Table 3. M = Mesial, B = Buccal, D = Distal, L = Lingual, F = Fused, Bi = bifid apex. Ex: MLF = mesio-lingual fused roots, MLFBi = mesio-lingual fused roots with bifurcation. Congenitally absent teeth not included in statistics for this table.

Canal shape and configuration

Single round (R) and ovoid (O) canals are the most common canal morphologies and configurations in nearly all teeth of both jaws (Table 10). Interestingly, R canals are most prevalent in maxillary teeth while O canals are most prevalent in mandibular teeth. Isthmus canals (i2-i5) appear with less frequency than single (R and O) and double-canaled (R2-R5) variants and are mostly found in the mandibular molars. The double-canaled R5 orientation appears the least. No R3 variants appear in this sample.

Table 10: Number of canal shapes and configurations in the maxilla and mandible by tooth

Tooth	Canal morphology	n˜	% of canals†	Tooth	Canal morphology	n˜	# of canals†
Maxilla				**Mandible**			
I^1	O	22	10.78	**I_1**	O	110	48.25
	R	182	89.22		R	70	30.70
					R2	5	4.39
					R4	18	15.79
					i2	1	0.88
I^2	O	84	33.73	**I_2**	O	140	56.68
	R	163	65.46		R	68	27.54
	R4	1	0.80		R2	6	2.43
					R4	31	12.55
					i2	1	0.40
					i5	1	0.40
C^1	O	227	55.77	**C_1**	O	204	64.35
	R	178	43.74		R	73	23.03
	R5	1	0.49		R2	1	0.63
					R4	15	9.46
					R5	1	0.63
					i2	3	1.89
P^3	O	67	6.99	**P_3**	O	177	40.69

	R	458	47.76		R	84	19.31
	R2	120	25.03		R2	21	9.66
	R4	75	15.64		R4	1	0.46
	R5	7	1.46		i2	2	0.92
	i2	6	1.25		i3	1	0.46
	i5	9	1.88		i4	2	1.38
					i5	59	27.13
P^4	O	193	27.26	**P_4**	O	179	54.91
	R	163	23.02		R	121	37.12
	R2	70	19.77		R2	5	3.07
	R4	90	25.42		R4	1	0.61
	R5	3	0.85		i5	7	4.29
	i2	11	3.11				
	i5	2	0.56				
M^1	O	357	14.69	**M_1**	O	225	15.83
	R	1,379	56.75		R	142	9.99
	R2	149	12.26		R2	261	36.73
	R4	134	11.03		R4	86	12.10
	R5	14	1.15		R5	5	0.70
	i2	33	2.72		i2	105	14.78
	i3	3	0.25		i3	30	4.22
	i4	1	0.08		i4	10	1.41
	i5	13	1.07		i5	30	4.22
M^2	O	284	14.87	**M_2**	O	295	26.66
	R	1,245	65.18		R	90	8.13
	R2	53	5.55		R2	139	25.11
	R4	69	7.23		R4	99	17.89
	R5	4	0.42		R5	2	0.36
	i2	45	4.71		i2	68	12.29
	i3	7	0.73		i3	22	3.97
	i4	1	0.16		i4	12	3.25
	i5	11	1.15		i5	13	2.35
M^3	O	120	11.27	**M_3**	O	202	27.01
	R	740	69.48		R	185	24.73
	R2	44	8.26		R2	58	15.51
	R4	25	4.69		R4	72	19.25
	i2	21	3.94		i2	31	8.29
	i3	3	0.56		i3	5	1.34
	i4	1	0.28		i4	1	0.40
	i5	8	1.50		i5	13	3.48

~ n column list times each variant appears. However, R2, R4, R5, and i2-i5 are two-canaled variants and are counted twice to calculate % of canals. † = Table 4. Congenitally absent teeth not included in statistics for this table.

Classification system

As discussed in the literature review above, the categorization of roots and canals can be misleading or inaccurate when systems limited to tooth/canal type are applied to other root/canal types. Problematically, classification scheme exists that captures all components of the complete tooth root phenotype. We have presented here a new system that is simple, accurate, human and computer readable, and allows for easy qualitative and/or quantitative analysis of the entire phenotype, or each of its constituent parts, individually or in any combination. We have outlined five phenotypic elements (E) that comprise the human tooth root phenotype: E1 - root number, E2 - canal number, E3 – canal location, E4 - external morphology, and E5 – canal morphology and configuration. The system provides codes for each element, and the resulting combination constitutes that root complex's complete phenotype code.

Tooth name or number

Our system works with categorical and numbering systems including, but not limited to, the Palmer Notation Numbering system, the FDI World Dental Federation System, simple abbreviations such as UP4 (upper 2^{nd} premolar) or LM1 (lower first molar), or the super- and subscript formulas described in and used throughout this study.

Root number or absence

Roots are recorded by simple counts and represented with an R. For example, a two-rooted tooth would be coded as R2. Root number is determined using the Turner index [1] as outlined in the methods section. In the case of congenitally absent teeth and roots we use CON, rather than 0 or NA. This is because congenital absence of a tooth is a heritable phenotypic trait, with different population frequencies [86,87]. In the case of missing teeth, root number can often be recorded by counting the alveolar sockets. Fig 13 presents a workflow for recording E1 and its variants.

Fig 13. **Flow chart for determining and recording phenotype element 1 - root number or absence.**

Canal number

Like root number, canal number is a simple count but represented with a C rather than an R. As discussed in the methods section, we apply the Turner index (1991), essentially a system of thirds, to determine counts. Building the above example, a two rooted, three canaled tooth would be coded as R2-C3. Fig 14 presents a workflow for recording E2 and its variants.

Fig 14. **Flow chart for determining and recording phenotype element 2 - canal number.**

Anatomical locations of canals

The locations of the canals in the root complex are easily recorded following the anatomical directions common to any dental anatomy textbook and discussed above. Fig 15 presents a workflow for recording E3 and its variants. Labeling order begins with mesial (M), followed by buccal (B), distal (D), and lingual (L), inclusive of intermediate locations (e.g., mesio-distal). Continuing the above example, if two canals are found in the mesial root and one in the distal root, the root complex would be coded as R2-C3-M2D1.

Fig 15. **Flow chart for determining and recording phenotype element 3 - anatomical location of canals.** Bottom left: Axial CT scan slice of right maxillary dental arcade. Anatomical directions: A = axial, M = mesial, MB = mesio-buccal, B = buccal, BD = bucco-distal, D = distal, DL = disto-lingual, L = lingual, ML = mesio-lingual, F = fused.

External Root Morphology

Fig 12 and Table 6 visualize and describe external root morphologies recorded at the midpoint of the root, while Fig 16 presents a workflow for recording E4 and its variants. Fused roots also fall under E4. However, unlike the morphologies described in Table 6 and Fig 12, fused roots are simply recorded with F (for fused) appended to the anatomical locations of the fused roots. For example a mesial and buccal fused root, would be recorded as MBF. Though we have used axial slices to determine these morphologies, they can be ascertained visually from extracted teeth, and occasionally the alveolar sockets of missing teeth [2]. A tooth with two roots, containing three canals – two in the mesial root and one in the distal root, with an hourglass and plate shaped mesial and distal roots, is coded as: R2-C3-M2D1-MHDP.

Fig 16. **Flow chart for determining and recording phenotype element 4 - external root morphology.**
*if root is bifurcated, append morphology with Bi. Ex: P = plate, PBi = plate-bifurcated. Right: axial CT slices showing external root morphologies.

Canal configuration

Fig 17. **Flow chart for determining and recording phenotype element 5 - canal morphology and configuration.** Right: sagittal CT slices showing canal morphologies. *Because the R3 variant does not appear in this sample, the sagittal slice is represented by an illustration.

Root canal configuration requires visualization of the canal system from the CEJ to the foramen/foramina. While µCT or CBCT provide the greatest resolution for visualising these structures, in certain cases 2D radiography is sufficient (see Versiani et al., 2018 for an indepth discussion and comparison of techniques). Our simplified system (Figs 10 & 11) will help the user to classify accurately canal configurations as it is based on a system of thirds, rather than harder to visualize 'types'.

Fig 18. **Flow chart for determining and recording phenotype element 5 - canal morphology and configuration (isthmus canals).** Illustrations show external root morphologies including C-shaped root variants. Canal shape/configuration is in gray.

Figs 17 and 18 present a workflow for recording E5 and its variants. Finalizing the above example - two round canals in the mesial root and one ovoid canal in the distal root can easily be coded as MR2DO; completing the root complex phenotype code as: R2-C3-M2D1-MHDP-MR2DO (Fig 19).

Fig 19. **Five phenotypic elements of a lower left 1st mandibular molar (RM_1-R2-C3-M2D1-MHDP-MR2DO).** A. E1 - Root presence/absence; B. E2 - Canal presence/absence, C. E3 - Canal location, D. E4 - Canal morphology, E. E5 - Canal shape. Images A and B from the Root Canal Anatomy Project https://rootcanalanatomy.blogspot.com/ (accessed 10 March 2021)

Redundancy of information

There is a bit of redundancy of information in our system. For example, R2-C3-M2D1-MHDP-MR2DO can be shortened to MHR2-DPO without loss of information. MHR2 describes a mesial (M) root (1 root) that is hourglass (H) shaped with two round (R2) canals (C), while DPO describes a distal (D) root (1 root) that is plate (P) shaped, with one ovoid (O) canal (C). However, there are several issues with this shorter version. The first is that we designed to our system to record phenotype elements individually or in combination. MHR2 describes what is potentially a single rooted tooth or could be a four rooted tooth. R2 indicates that the root complex is two-rooted, as does M2D1, MHDP, and/or MR2DO. The second is human and computer readability. For a human, R2-C3-M2D1-MHDP-MR2DO is easier to read and understand than MHR2-DPO. For a computer, R2-C3-M2D1-MHDP-MR2DO allows easy separation and/or recombination of elements for analysis. The third is that not all users will have visual access to all elements within a root complex. It might be lack of equipment (radiography) or missing teeth. Thus, our system is also designed to capture the most information available to the user, missing information can be easily represented. Although there is a level of redundancy, the system is optimized for human and machine reading.

The phenotypic set within the morphospace of root diversity

Within these phenotypic elements, there is exist 841 unique phenotype element permutations derived from our global sample. These comprise our study's "phenotypic set" among the range of potential phenotypic permutations. Anterior teeth have the least number of permutations while molars, particularly maxillary molars, have the greatest (Fig. 20).

Fig 20. **Number of phenotypes in individual teeth.**

Discussion

This paper set out to present a method that would capture quantitatively and qualitatively the diversity of human tooth root phenotypes, using a modular approach. It has shown that it is possible to have a universal code for phenotyping roots, and that a global sample of modern humans demonstrates the high level of tooth root phenotype diversity. A more comprehensive set of tooth root data should reinforce and expand the broader toolset for studying human phenotypic diversity (e.g., tooth crowns, craniofacial morphometrics, genetics, etc.).

The large number of phenotypes permutations found in our sample can be explained by the variation within each element. For example, Table 10 shows how permutations in one element can result in four nearly identical tooth roots with four different phenotype codes. Here, all these roots are identical in their phenotypic elements with the exception of their external morphology (E4). Teeth with more roots result in a greater number of permutations. Fig 21 illustrates how increasing numbers and multiple combinations, and orientations of root morphologies create the morphological permutations of the external phenotypic elements. However, compared to tooth crowns, the number of phenotype permutations is relatively few, as a recent test of ASUDAS crown traits indicates greater than 1.4 million combinations, or permutations of crown phenotypes [88].

Table 10: Changing one element results in phenotype permutations in single-rooted teeth.

E1	E2	E3	**E4**	E5	Code
R1	C1	A	**P**	O	R1-C1-A-P-O
R1	C1	A	**E**	O	R1-C1-A-E-O
R1	C1	A	**W**	O	R1-C1-A-W-O
R1	C1	A	**K**	O	R1-C1-A-K-O

Fig 21. **Variation in the tooth root complex.** Left - Combinations of individual root types form multiple root complexes (e.g., C3 = one tooth with two plate shaped roots). Right - multiple root forms can appear in the tooth row. The left panel shows the range of possible combinations, while the right provides an example.

We would emphasize two elements of the approach. The first is the expansion of data available and the use of a universal and modular system. Scanning technologies have provided greater access to tissues, such as tooth roots, that were previously difficult to access for visual inspection, thus, permitting a much fuller and complete description of these morphologies. The system we have developed is designed to be comprehensive and universal, so that any tooth can be placed within the set of attributes. The five phenotypic elements - root presence/absence (E1), canal root presence/absence (E2), canal location (E3), external root morphology (E4), and canal morphology and configuration (E5), allow for independent categorization, so that phenotypes can be put together combinatorically, or treated as individual components – for example, using just external root morphology. Although constructed for recent human variation, we have shown through preliminary case studies that the system can be extended across extant and fossil hominids, providing an additional tool for reconstructing evolutionary history, as well be used to map geographical patterns among contemporary human populations. Its broader applicability will be dependent upon an expansion in the number of scans available; while this is increasingly the case for fossil hominins, more regular scanning of more recent samples will be essential for studies of human diversity.

The advantages of this system, in addition to its universality, is that it allows for relatively simple qualitative and quantitative analysis. This is important, as there is increasing interest in mapping human diversity in different ways, using quantitative techniques [89–91]; the abundance of dental remains provides an additional source of information. In addition, there is growing interest among geneticists to map phenotypic variation against genetic variation [92], and to develop a better understanding of genotype-phenotype relationships. As teeth are generally to be considered strongly influenced by their genetic components [93,94], they are an ideal system for testing these relationships. It may be the case that different phenotypes behave differently across populations, and so tooth roots can become part of phenotype-genotype comparisons. Such comparisons can be either phenetic, or phylogenetic, as the coding system is entirely suitable for cladistic analysis.

The second element relates to morphospace, an increasingly utilized concept in evolutionary biology [95,96]. The morphospace is the total available forms that a phenotype can take, limited by physical or biological properties. Evolution is, in a sense, following paths in morphospace [97]. The phenotypic set is that part of the morphospace that is actually occupied. The method proposed here has explored the available morphospace for human tooth roots and has provided a series of elements that describe it. There are a very large number of possible phenotypes under this system (in principle, the total number is combinatorial product of the five phenotypic elements and their potential states, although in practice the number would be much smaller due to functional and physical constraints), but we have shown here that in a relatively large sample there are about 841 observable individual tooth phenotypes – in other words a small proportion of possible ones. What is critical here is that the proposed method allows the realized and potential phenotypic sets of dental roots to be determined and analysed in potential evolutionary, developmental and functional contexts.

Finally, for the method to be worthwhile, it is necessary for it to be useful in relation to current hypotheses and research foci. Four are immediately apparent. First, current interest in the role of dispersals, not just the initial one from Africa [98–100], but also the increasing genetic evidence for multiple later regional dispersals means that finding ways of linking the palaeoanthropological and archaeological record to the inferred genotypes requires diverse phenotypes, and methods such as this will be required [101–104]. The second is in terms of earlier phases of human evolution; with the current evidence for interbreeding across hominin taxa [105], it is necessary to have appropriate phenotypic systems – and roots are likely to be a good one – to tease out the phenotypic effects in such admixture [106,107]. Third, there is considerable interest in modularity and integration in evolution, and the modular approach adopted here may provide a suitable model system for exploring these issues [108,109]. And finally, biomechanical and spatial studies of the hominid masticatory system can draw quantitative functional and dietary inferences from root and canal number and morphology [110–113].

Conclusions

Compared to tooth crowns, tooth roots have received little attention in evolutionary studies. Novel technologies have increased the potential for exploiting variation in root morphology, and thus increased their importance as phenotypes. This paper presents a novel method for defining and analysing the morphospace of the human tooth-root complex. The five phenotypic elements of the system root presence/absence (E1), canal root presence/absence (E2), canal location (E3), external root morphology (E4), and canal morphology and configuration (E5), were designed to: 1) identify the elements that best describe variation in root and canal anatomy, 2) create a typology that is modular in nature and can be appended for undocumented morphotypes, and 3) is applicable to hominoids. The system will provide a basis for future research in human evolution, human genotype-phenotype investigations, and the functional biology of the human masticatory system.

Acknowledgements

We would like to thank Drs. Marta Miraźon-Lahr, Francis Rivera, and Lynn Copes for access to, and permission to use their CT scan collections.

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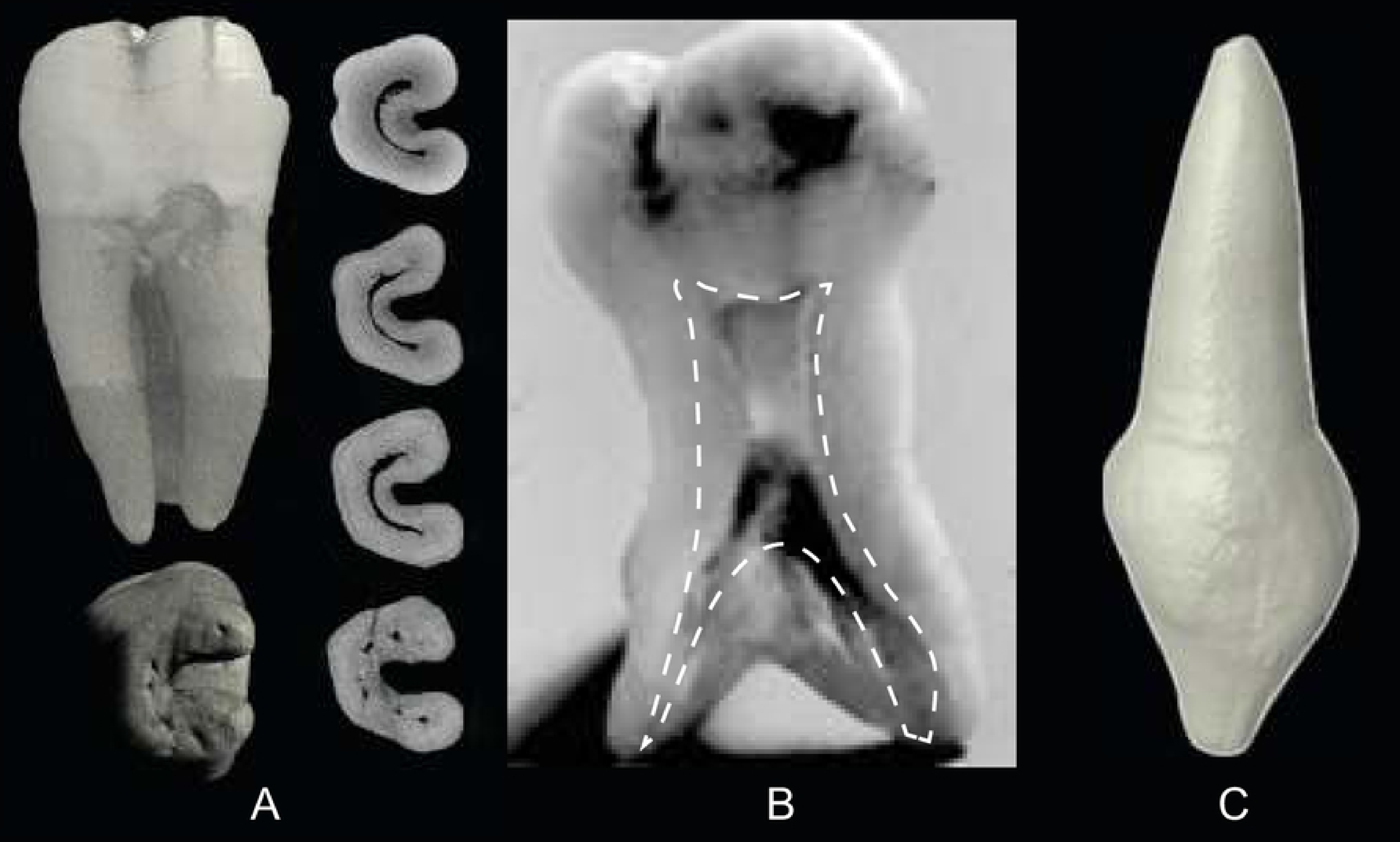
Supporting information

See S1 Table

A1 A2 B C D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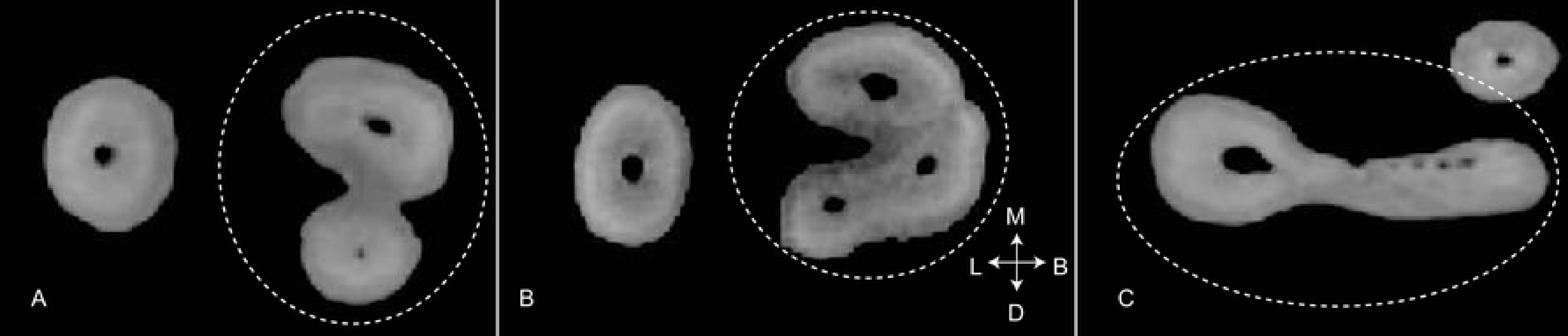
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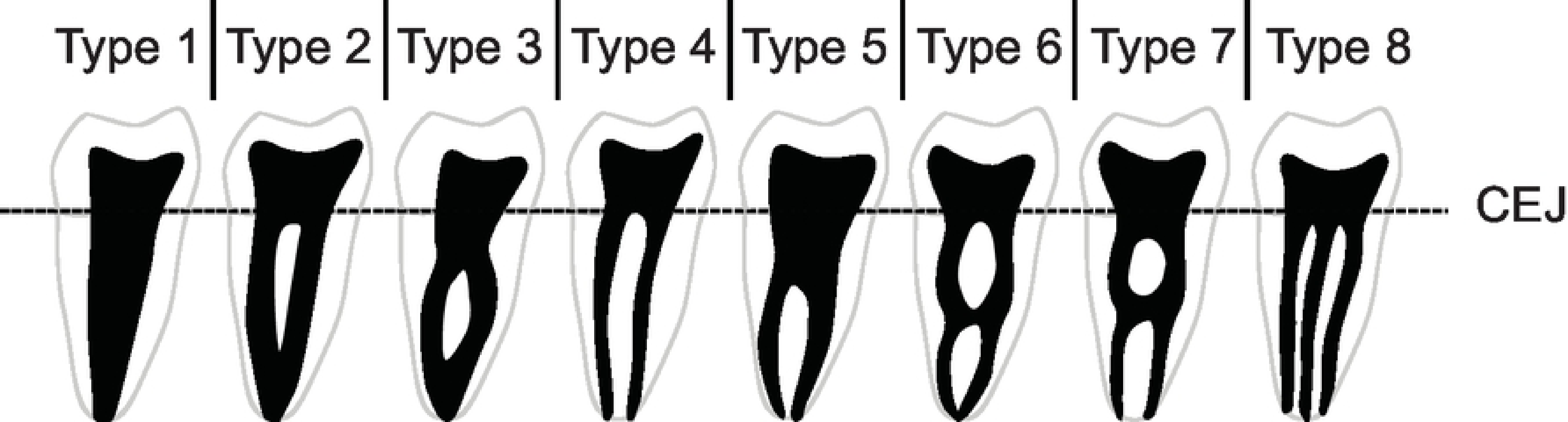
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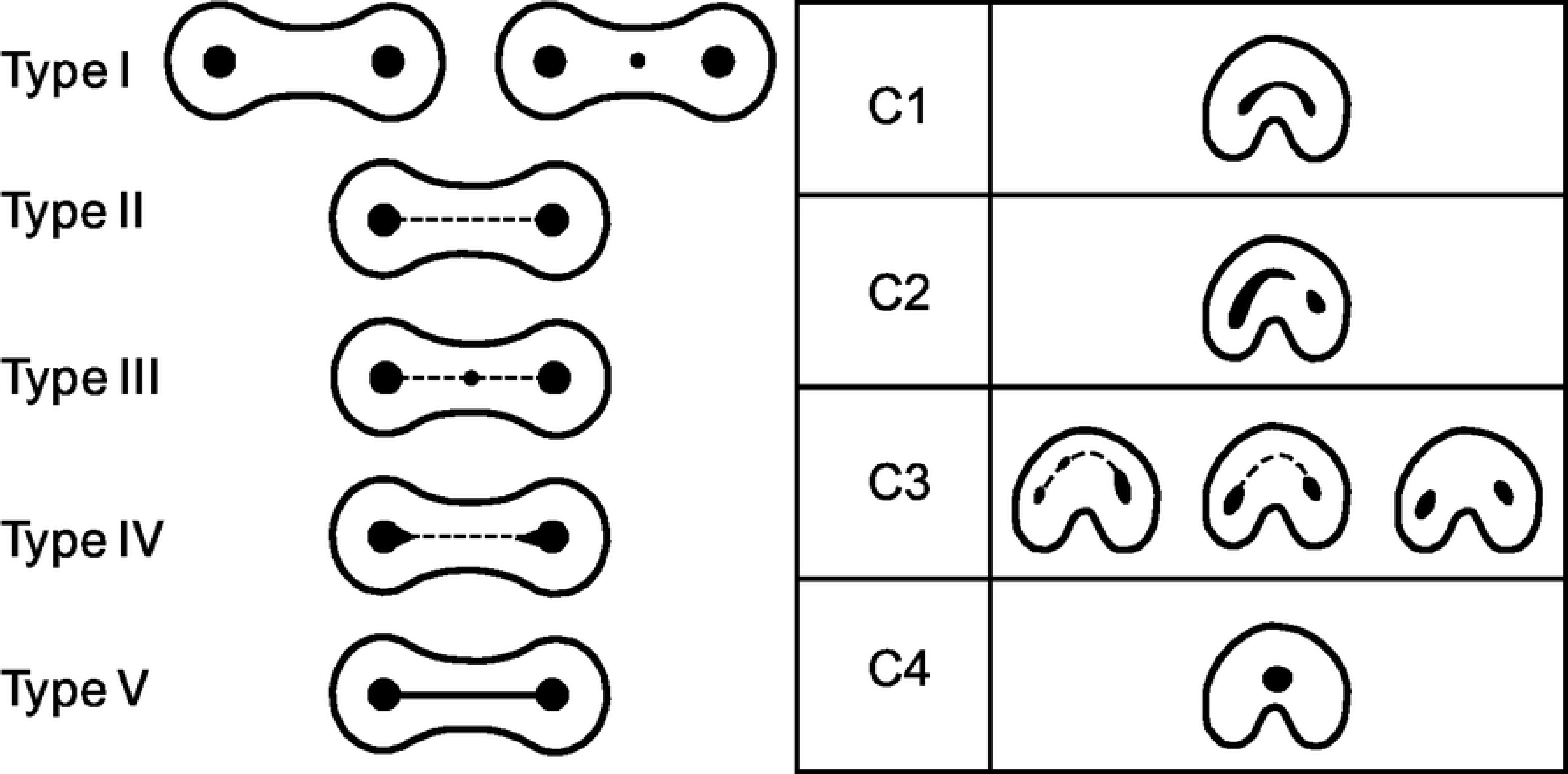
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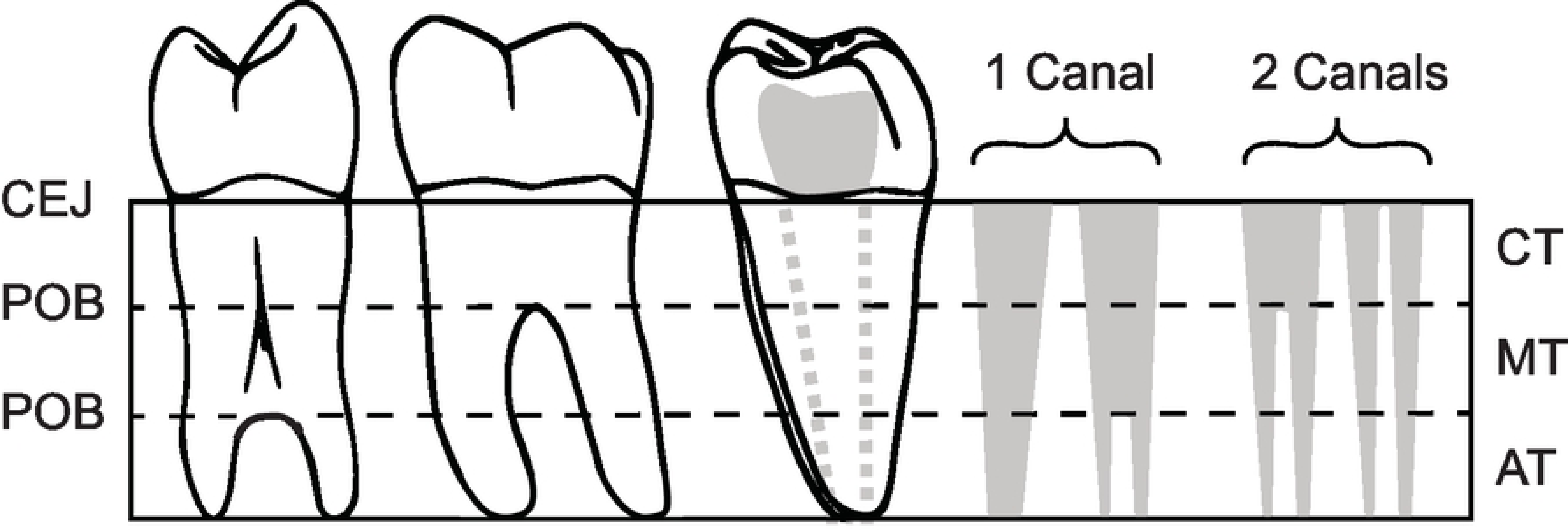
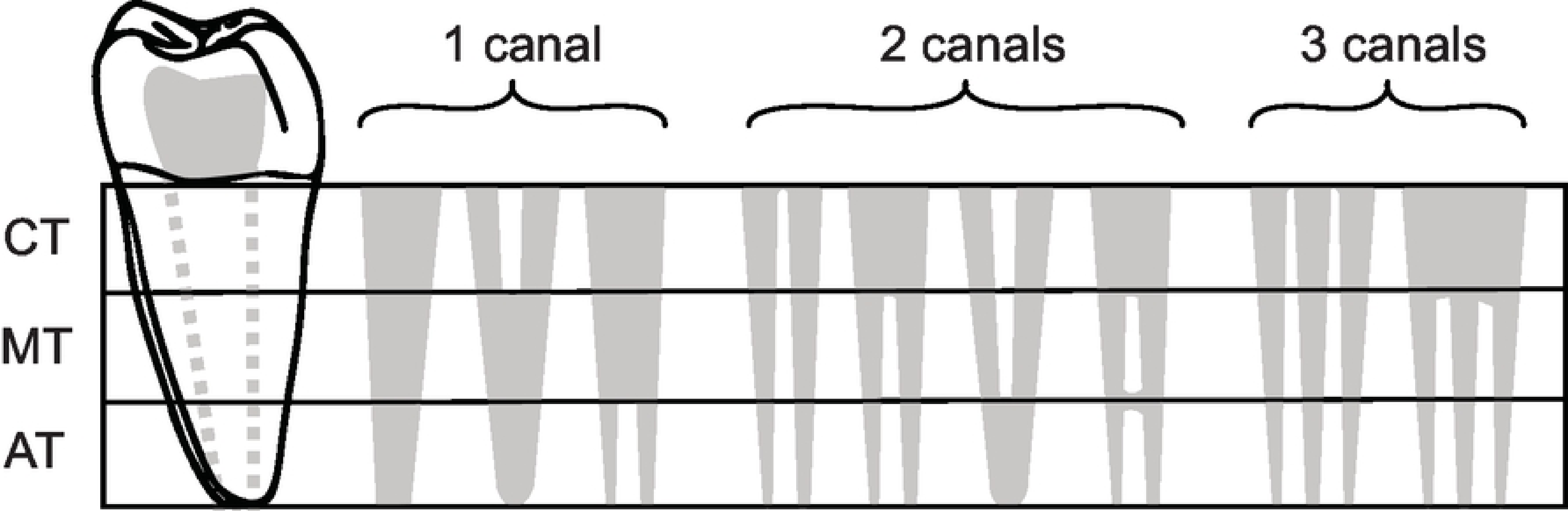
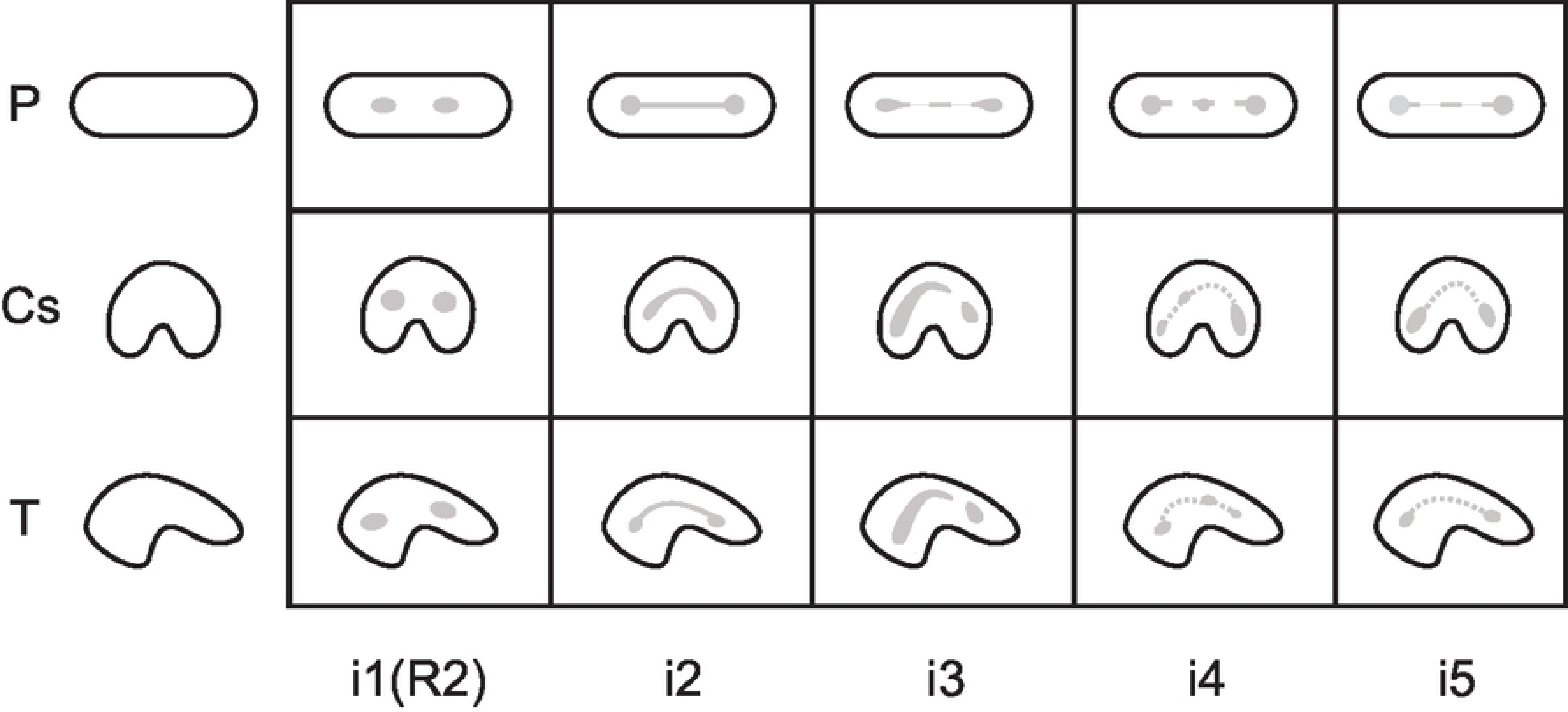
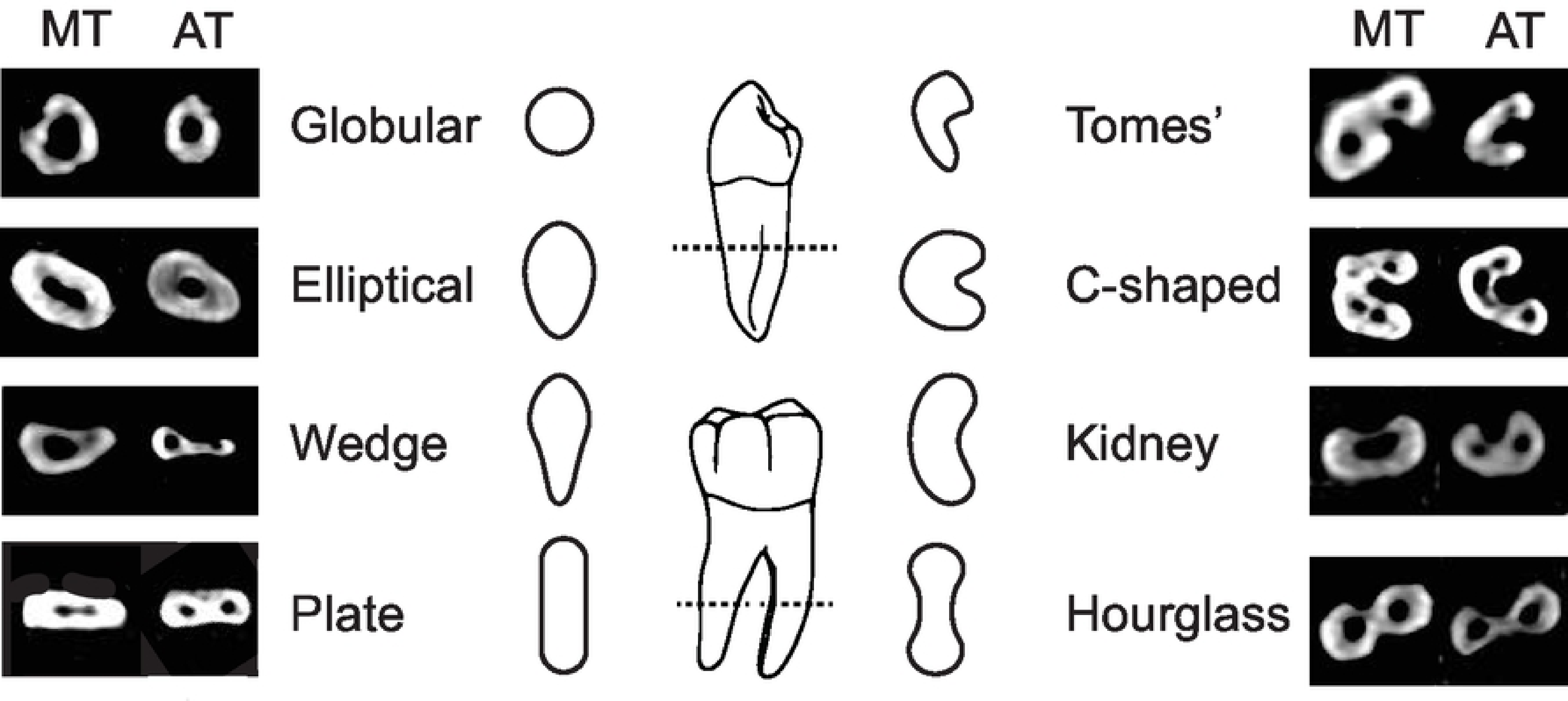
C3
C4

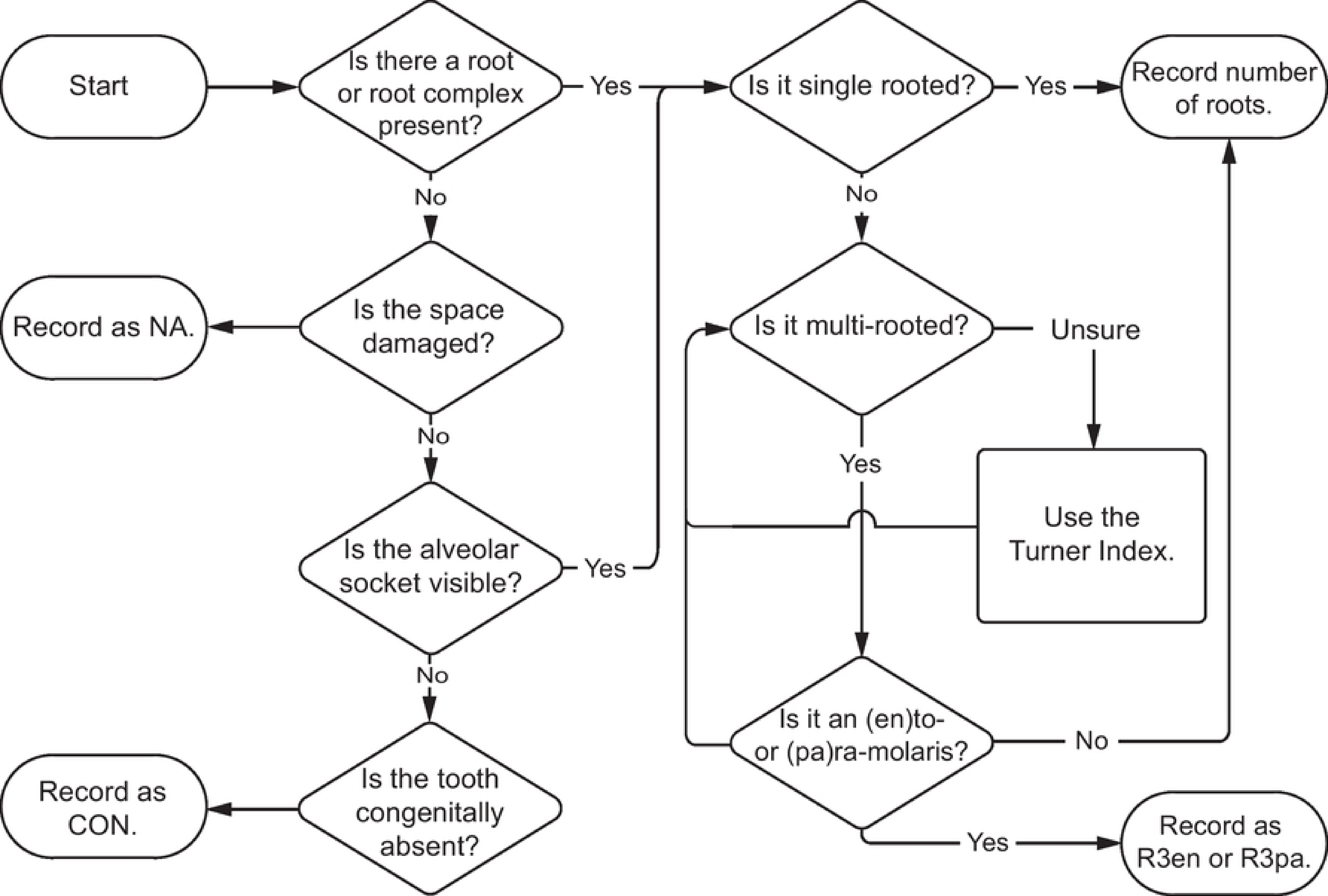

1 Canal
2 Canals
CEJ
POB
POB
CT
MT
AT

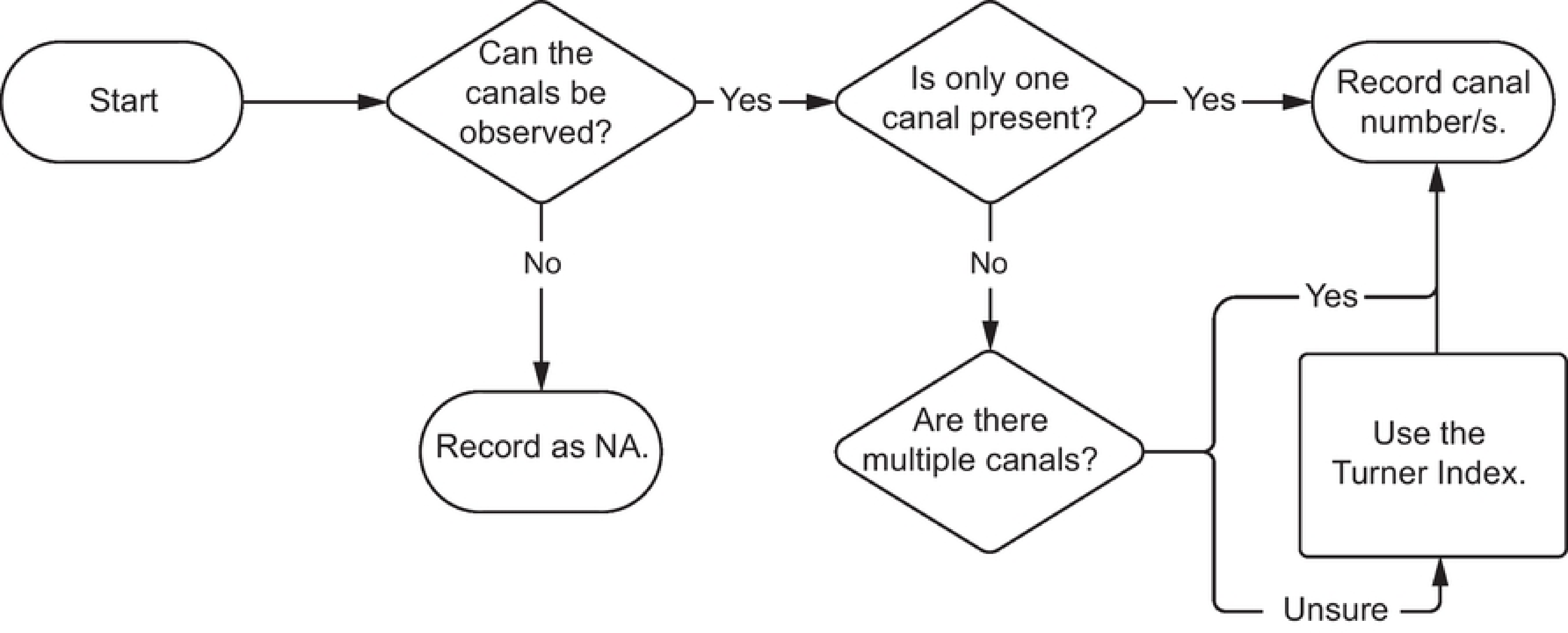

R
O
R2
R3

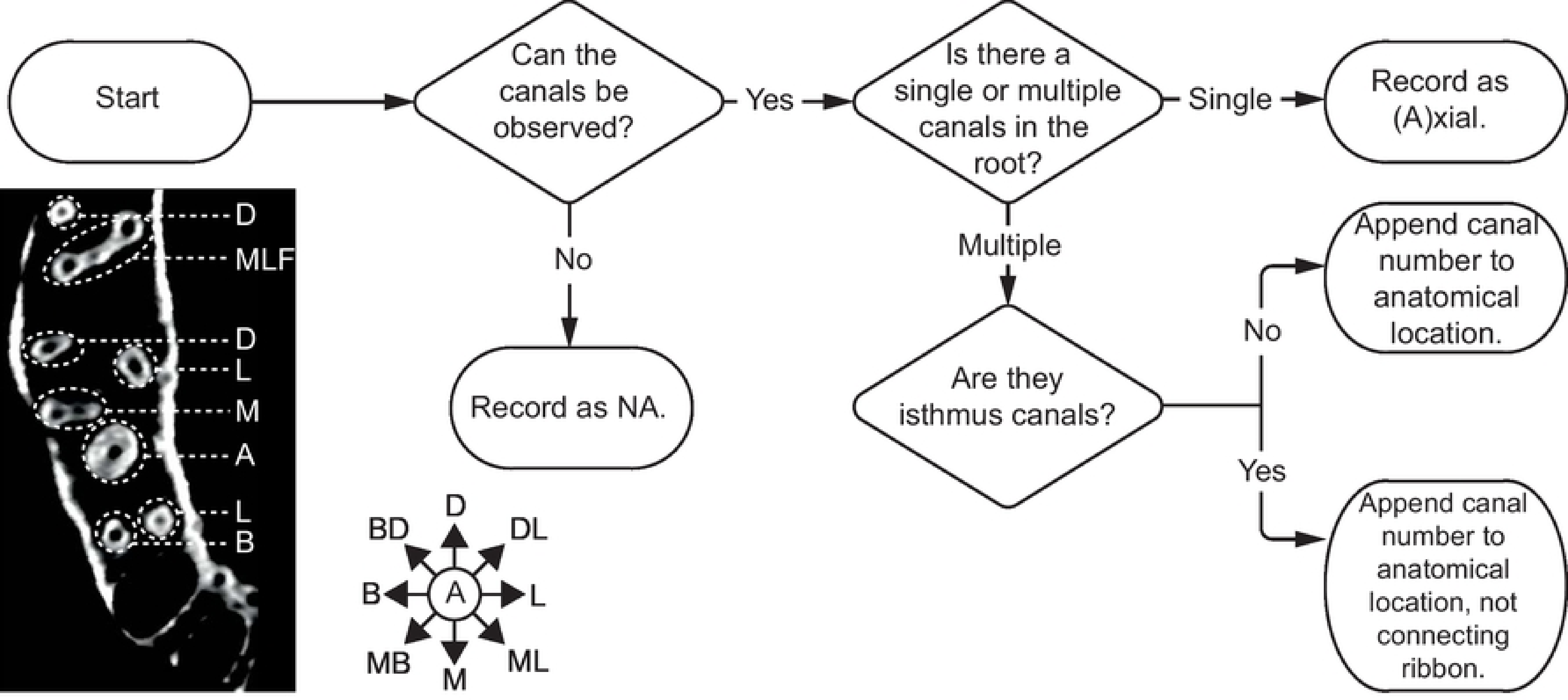

1 canal
2 canals
3 canals
CT
MT
AT

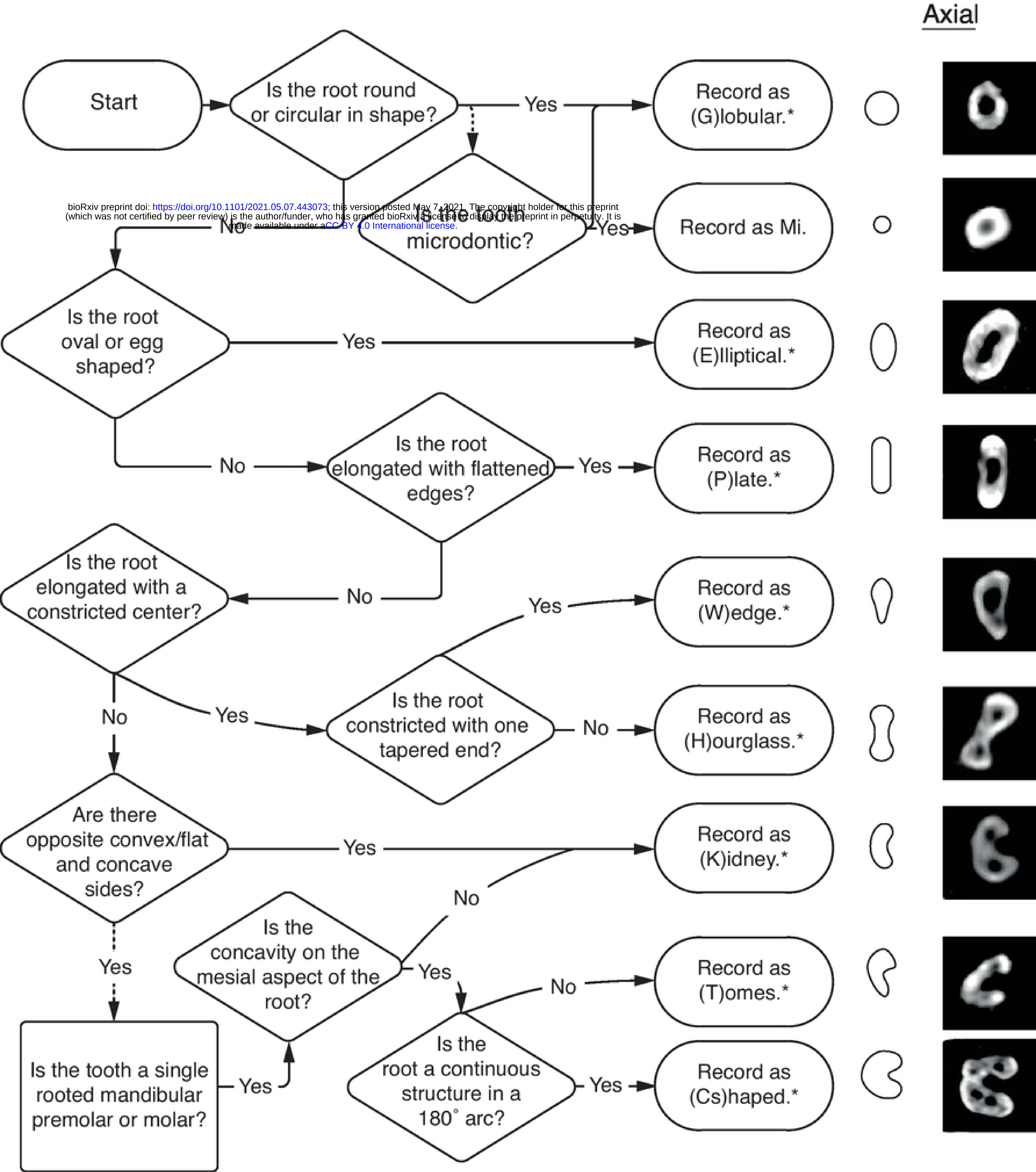

P
Cs
T
i1(R2)
i2
i3
i4
i5

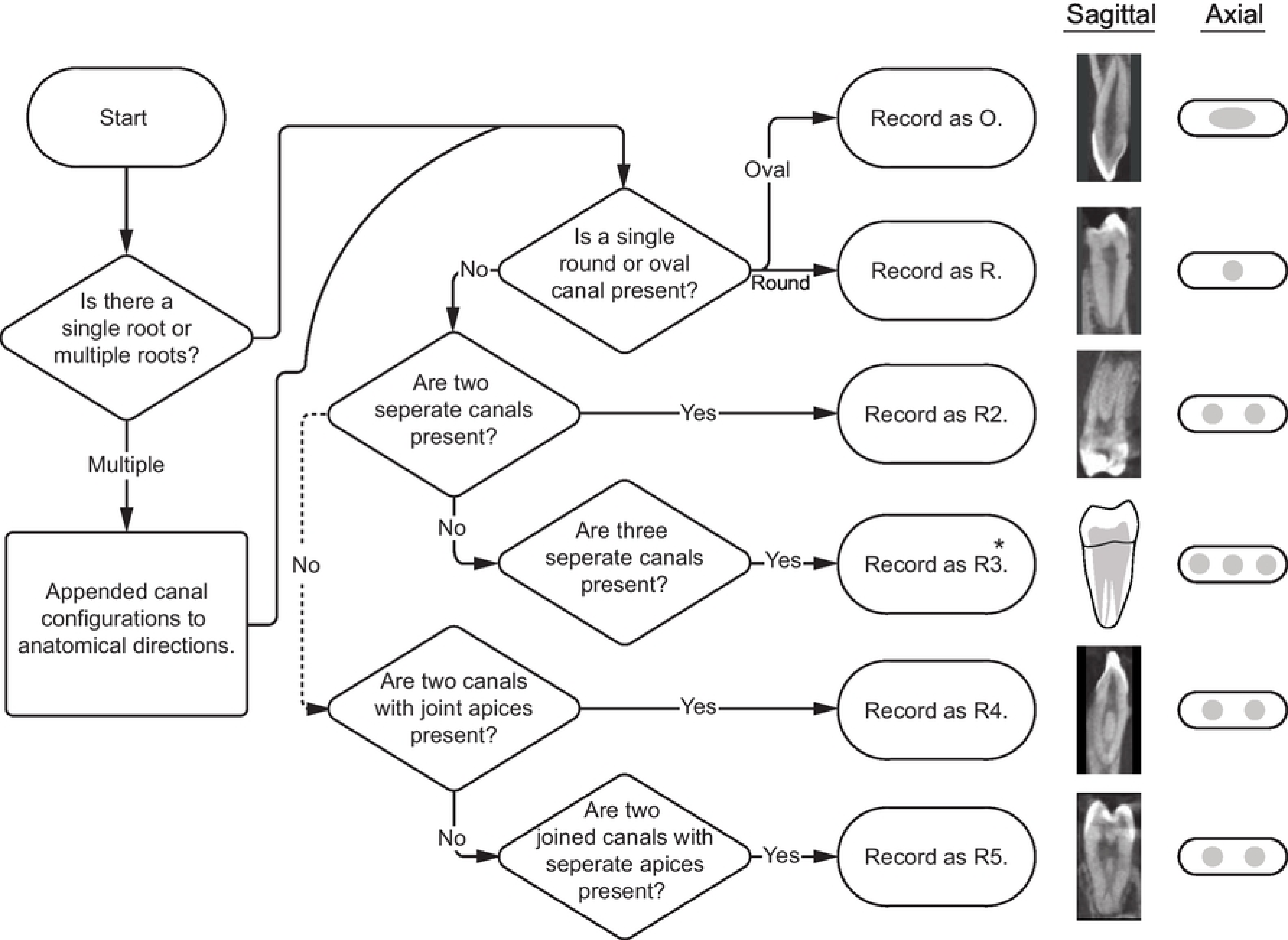

MT
AT
Globular
Elliptical
Wedge
Plate
MT
AT
Tomes'
C-shaped
Kidney
Hourglass

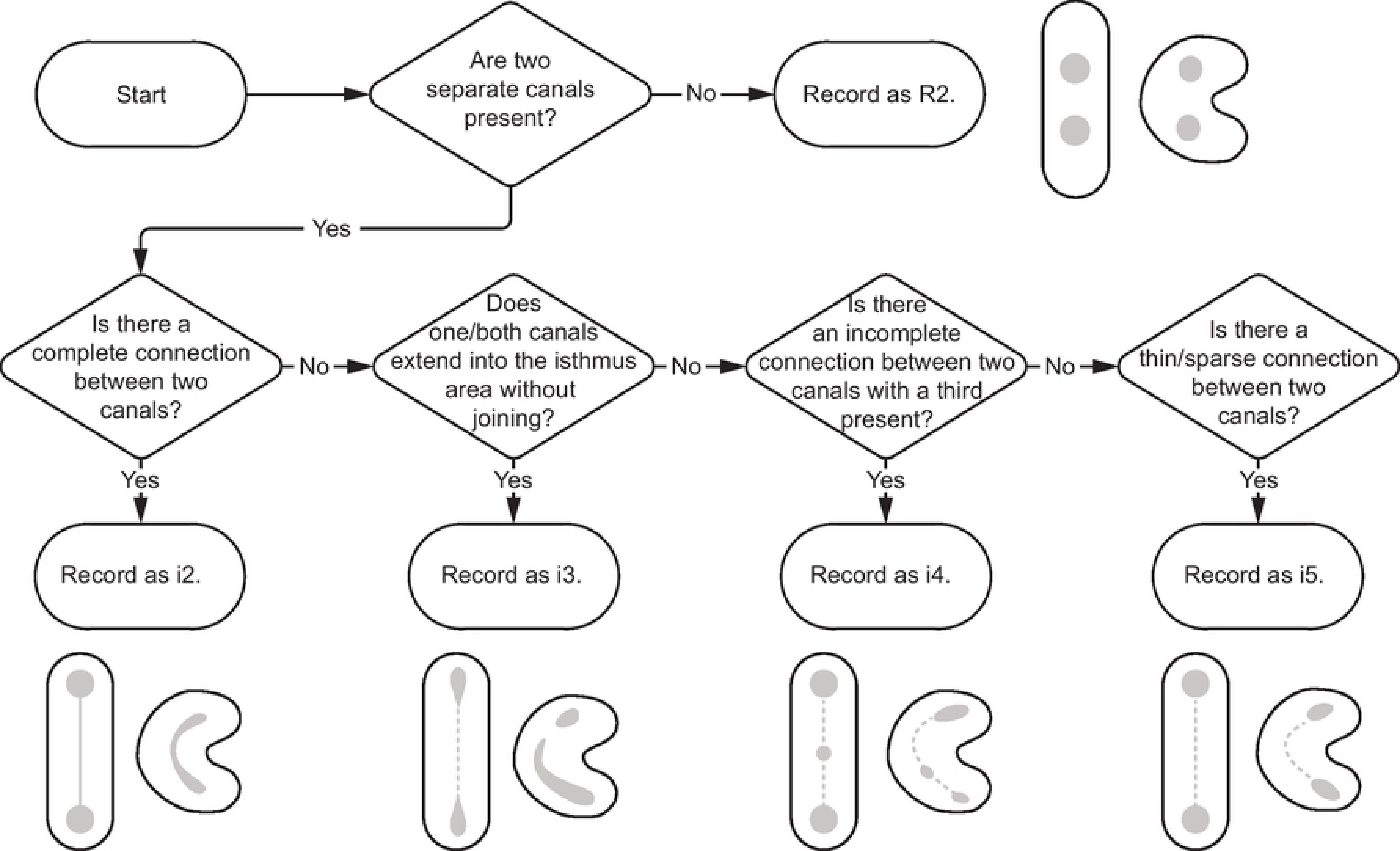

Start
Is there a root or root complex present?
Yes
No
Is the space damaged?
Record as NA.
No
Is the alveolar socket visible?
Yes
No
Is the tooth congenitally absent?
Record as CON.
Is it single rooted?
Yes
Record number of roots.
No
Is it multi-rooted?
Unsure
Use the Turner Index.
Yes
Is it an (en)to- or (pa)ra-molaris?
No
Yes
Record as R3en or R3pa.

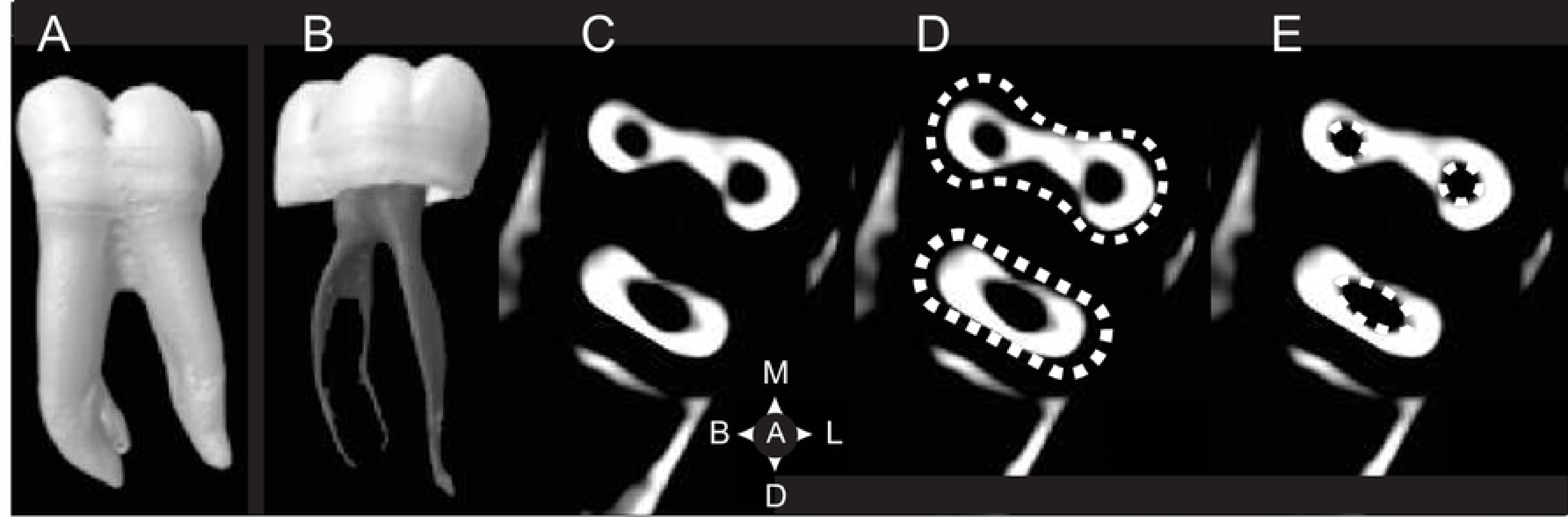

Start
Can the canals be observed?
Yes
No
Record as NA.
Is only one canal present?
Yes
Record canal number/s.
No
Are there multiple canals?
Yes
Unsure
Use the Turner Index.


Start
Can the canals be observed?
Yes
No
Record as NA.
Is there a single or multiple canals in the root?
Single
Record as (A)xial.
Multiple
Are they isthmus canals?
No
Append canal number to anatomical location.
Yes
Append canal number to anatomical location, not connecting ribbon.
D
MLF
D
L
M
A
L
B
D
BD
DL
B
A
L
MB
M
ML

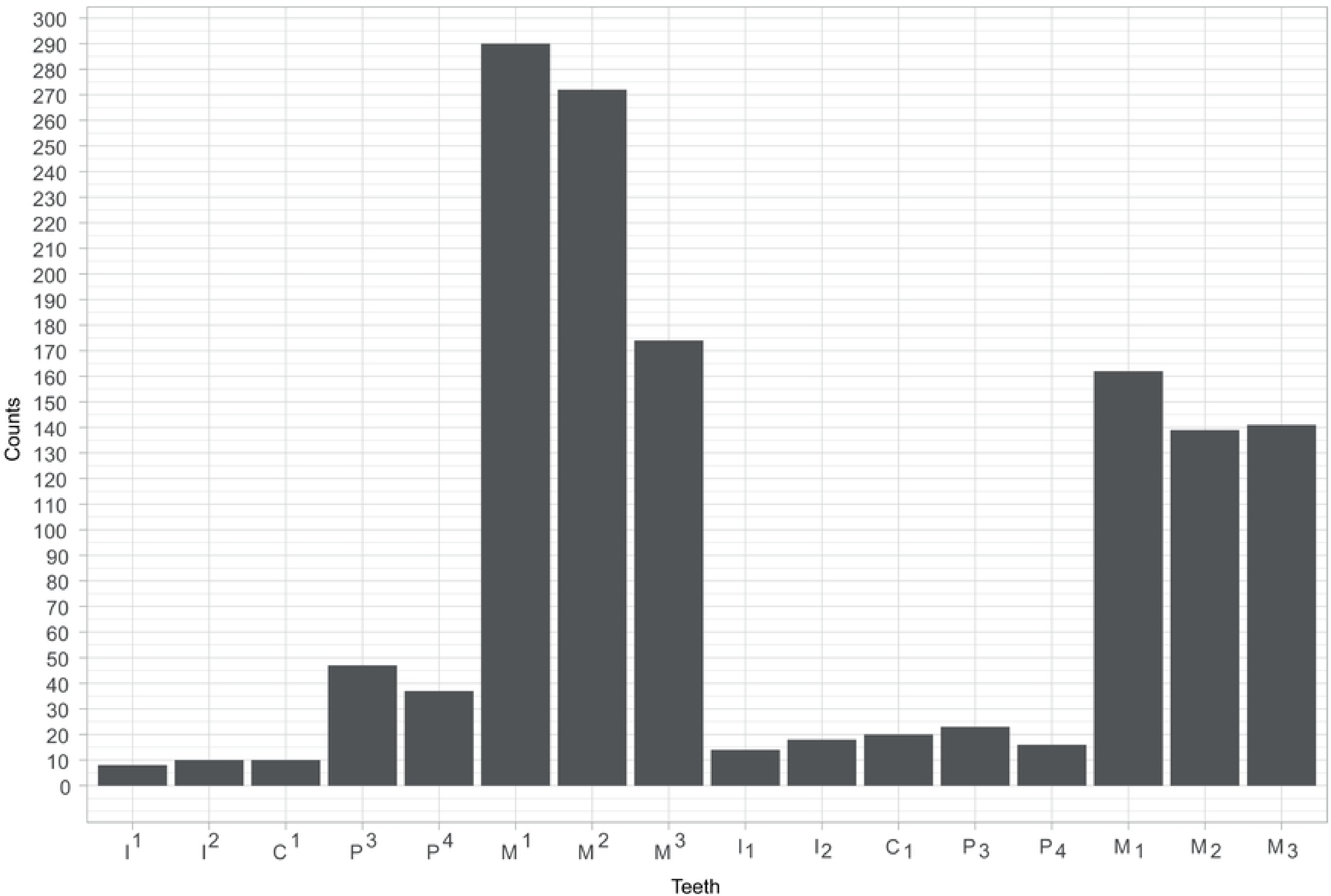

Axial
Start
Is the root round or circular in shape?
Yes
Record as (G)lobular.*
Is the tooth microdontic?
Yes
Record as Mi.
No
Is the root oval or egg shaped?
Yes
Record as (E)lliptical.*
No
Is the root elongated with flattened edges?
Yes
Record as (P)late.*
No
Is the root elongated with a constricted center?
Yes
Record as (W)edge.*
Yes
Is the root constricted with one tapered end?
No
Record as (H)ourglass.*
No
Are there opposite convex/flat and concave sides?
Yes
Record as (K)idney.*
No
Yes
Is the concavity on the mesial aspect of the root?
Yes
No
Record as (T)omes.*
Is the tooth a single rooted mandibular premolar or molar?
Yes
Is the root a continuous structure in a 180° arc?
Yes
Record as (Cs)haped.*


Sagittal
Axial
Start
Is there a single root or multiple roots?
Multiple
Appended canal configurations to anatomical directions.
Is a single round or oval canal present?
Oval
Round
No
Record as O.
Record as R.
Are two seperate canals present?
Yes
Record as R2.
No
Are three seperate canals present?
Yes
Record as R3.*
No
Are two canals with joint apices present?
Yes
Record as R4.
No
Are two joined canals with seperate apices present?
Yes
Record as R5.

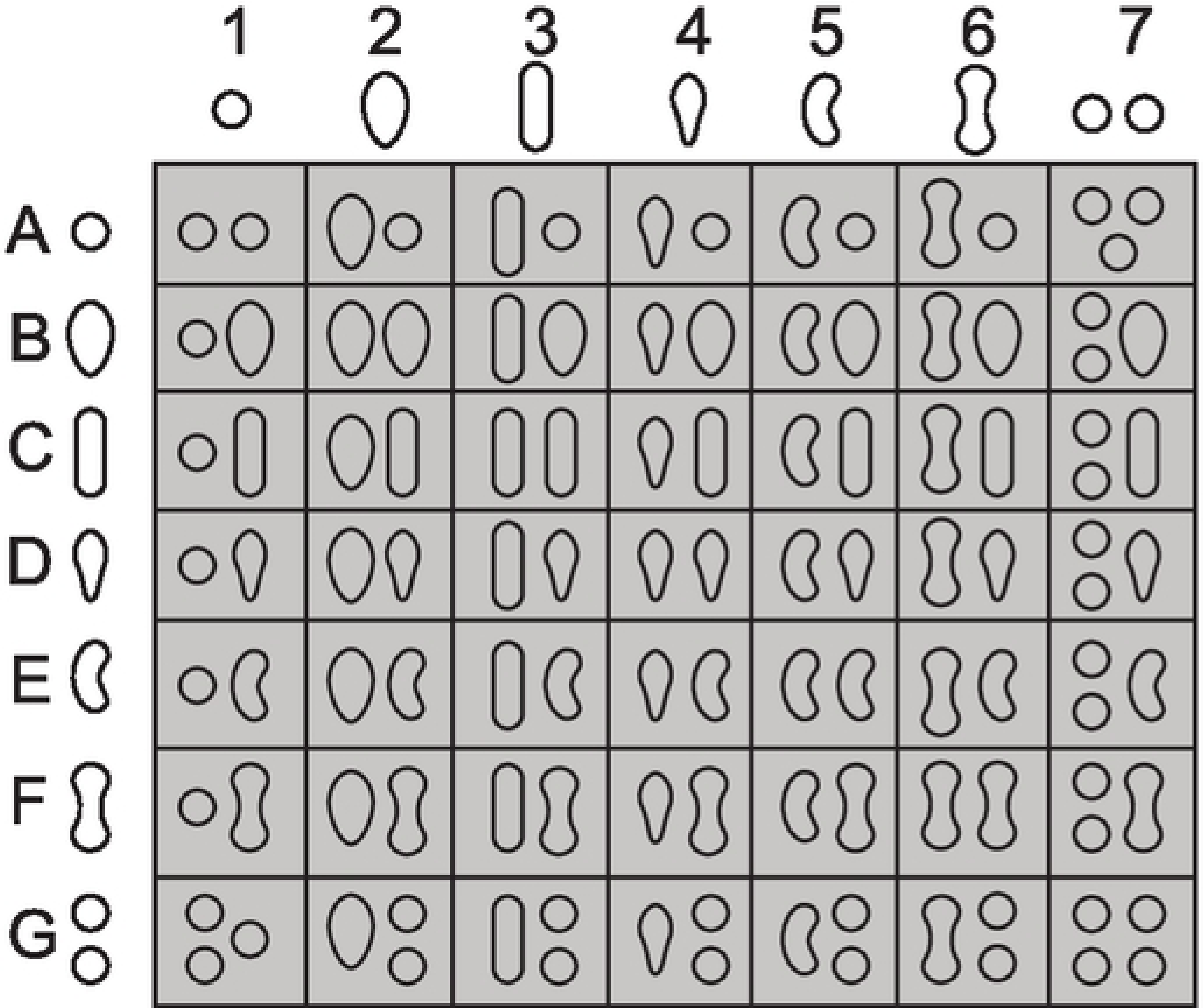

Start
Are two separate canals present?
No
Record as R2.
Yes
Is there a complete connection between two canals?
No
Does one/both canals extend into the isthmus area without joining?
No
Is there an incomplete connection between two canals with a third present?
No
Is there a thin/sparse connection between two canals?
Yes
Yes
Yes
Yes
Record as i2.
Record as i3.
Record as i4.
Record as i5.

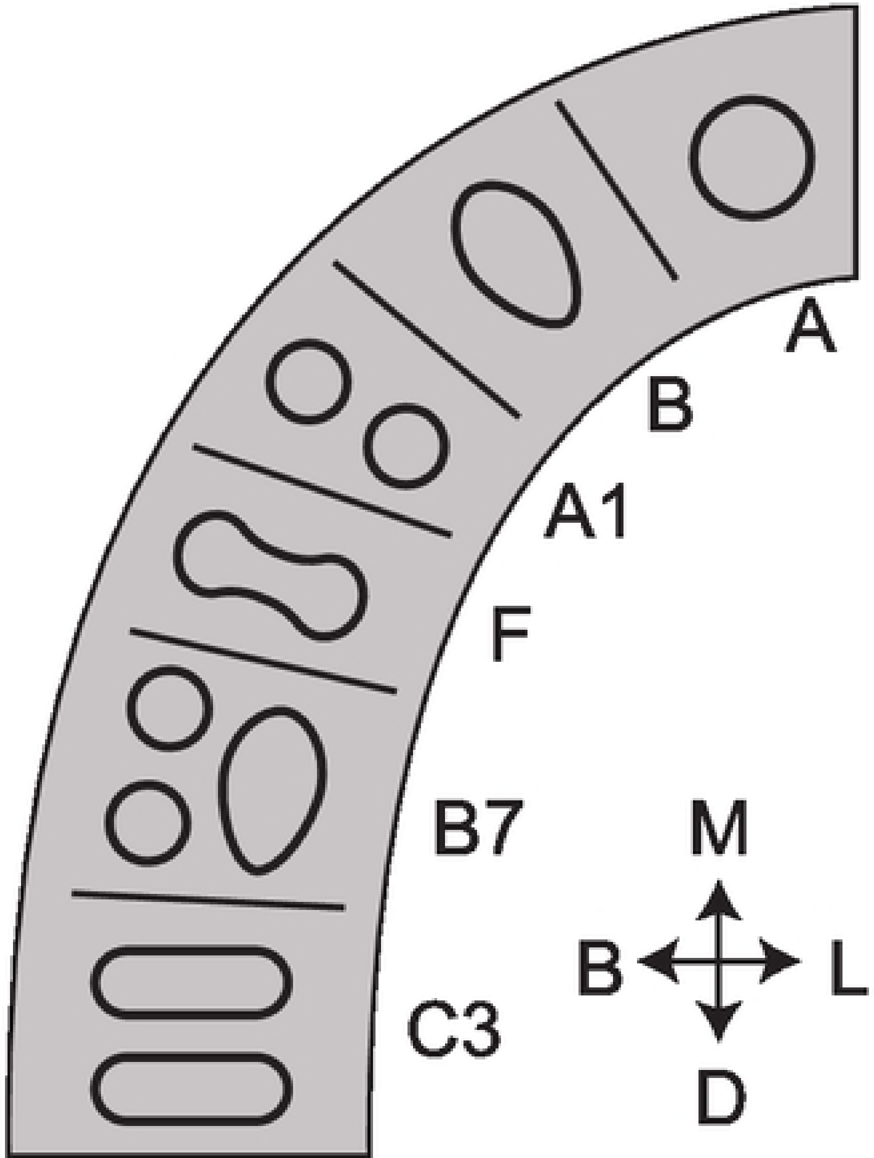


A
B
C
D
E
M
B
A
L
D



Counts
300
290
280
270
260
250
240
230
220
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
I^1
I^2
C^1
P^3
P^4
M^1
M^2
M^3
I_1
I_2
C_1
P_3
P_4
M_1
M_2
M_3
Teeth


1
2
3
4
5
6
7
A
B
C
D
E
F
G


A
B
A1
F
B7
C3
M
B
L
D