

A novel system for classifying tooth root phenotypes

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1 Abstract

2
3 Human root and canal number and morphology are highly variable, and internal root
4 canal form and count does not necessarily co-vary directly with external morphology. While
5 several typologies and classifications have been developed to address individual
6 components of teeth, there is a need for a comprehensive system, that captures internal
7 and external root features across all teeth. Using CT scans, the external and internal root
8 morphologies of a global sample of humans are analysed (n=945). From this analysis a
9 method of classification that captures external and internal root morphology in a way that is
10 intuitive, reproducible, and defines the human phenotypic set is developed. Results provide
11 a robust definition of modern human tooth root phenotypic diversity. Our method is
12 modular in nature, allowing for incorporation of past and future classification systems.
13 Additionally, it provides a basis for analysing hominin root morphology in evolutionary,
14 ecological, genetic, and developmental contexts.

15 16 Introduction

17
18 Human dental morphology is a diverse collection of non-metric traits: cusp numbers,
19 fissure and ridge patterns, root number and shape, and even congenital absence. Recording
20 systems, such as the widely utilized Arizona State University Dental Anthropology System
21 (ASUDAS) [1,2], have been developed to catalogue these traits and their variants under a
22 standardized scoring procedure; and to study how these variants are partitioned within and
23 between populations. However, dental trait scoring systems are overwhelmingly focused on
24 tooth crown morphology, with less attention paid to roots. Like tooth crowns, roots exhibit
25 considerable variability in number, morphology, and size. For example, premolars have been
26 reported as having between one to three roots [3,4], while maxillary and mandibular molars
27 have between one and five roots [5–8]. The literature has also long recognized several
28 unusual morphological variants such as Tomes' root [9], taurodont roots [10], and C-shaped
29 roots [11]. Additionally, the diversity of the canal system, both in number and configuration,
30 has been an area of extensive study (Table 1).

31 As the number of catalogued external and internal morphologies grow, there is an
32 increasing need for a comprehensive system, that can be used for documented and new

33 morphotypes, and is robustly capable of describing the total human tooth root phenotype.
34 The aim of this study is to 1) systematically describe the diverse internal and external
35 morphologies of the human tooth root complex (i.e., all roots present in an individual
36 tooth); and 2) define, develop, and provide a comprehensive system that captures these
37 morphologies in all the teeth of both jaws for analysis.

38 **Background**

39
40 The studies discussed below have addressed root number, canal number, external
41 root morphology, canal morphology, and canal configuration independently. However, they
42 comprise only parts of the tooth root complex, and thus provide a basis for a
43 comprehensive phenotype system.

44 **Root number**

45 Root number is probably the best studied element of root morphology, as counting
46 roots is easily accomplished in extracted and in-situ teeth. Early studies of roots were
47 primarily descriptive of root number, and the occasional metrical analysis [12,13,22–26,14–
48 21]. Maxillary premolars are reported as having the most variation in number of roots, with
49 a higher percentage of P³s having two roots (or at least bifurcated apices), while P⁴ is
50 typified by one root. Three rooted maxillary premolars (P³ and P⁴) have been documented in
51 modern humans [4,17,18,20,27,28] but are extremely rare. Scott and Turner [2] report a
52 world frequency of 4.9-65% for two-rooted premolars. Their results show that Sub-Saharan
53 Africans have the highest frequency at 65%, 40% in West Eurasian populations, 20-30% in
54 East Asian populations, and 5-15% in Northeast Siberians and Native Americans. In contrast
55 to the maxilla, the most frequent form of mandibular P₃s and P₄s is single rooted; though P₃s
56 are occasionally two-rooted or, more rarely, three rooted [29–31].

57 Maxillary molars are generally three rooted; though molars with two, four [32,33]
58 and five [34] roots have been reported. Variation in root number has been recorded for
59 three rooted M²s; with Australian Aboriginals having the highest reported percentage at
60 95.8% [15]. Sub-Saharan Africans also have a high frequency of three-rooted M²s at 85%,
61 Western Eurasians and East Asians ranging from 50-70% and American Arctic populations
62 ranging from 35-40% [2]. Three European samples by Fabian, Hjelmmann, and Visser (in
63 [24]) report an average of 56.6%, in accordance with Scott and Turner [2]. Inuit populations

64 are lower with East Greenland populations at 23.7% [22] and 30.7-31.3% in two prehistoric
65 Alaskan populations [35].

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

75

76

77 **Fig 1. Examples of accessory roots.** Mandibular molars with A1 and A2: radix entomolaris
78 (left=distolingual surface, right = lingual surface), B: M₃ with radix entomolaris (lingual view),
79 C: M₁ with furcation root (buccal view), D: M₁ with fused radix paramolaris (buccal view).
80 Modified from Calbersen et al., [36].

81

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

90 Single rooted molars usually appear in three forms: C-shaped M_{2s}, taurodont M_{1s}-
91 M_{3s}, and pegged M^{3s}/M_{3s} (Fig 2, A-C). C-shaped molars are common in Chinese populations
92 with a frequency as high as 40% [41]. The trait has a low frequency of 0-10% in Sub-Saharan
93 Africans [42], 1.7% in Australian Aboriginals [15], and 4.4% in the Bantu (Shaw, 1931). Rare
94 in modern humans, taurodont molars occur when the root trunk and internal pulp cavity are
95 enlarged and apically displaced. This form was first classified by Keith [10] in *Homo*
96 *neanderthalensis*. Externally, taurodont roots are cylindrical in shape (Fig 2B). While
97 sometimes confused with C-shaped molars, taurodont roots lack an internal and external

98 180° arc, and are instead circular in cross-section, usually with a bifid apical third. Pegged
99 third molars are the most variable in size and morphology [35]. Their reduction has a genetic
100 component and patterned geographical variation [35,43]. Pegged third molar roots are
101 associated with a reduced crown, appear more frequently in the maxilla than the mandible,
102 and are circular in cross-section

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

111
112 Fig 2. **Unusual root forms.** A. C-shaped tooth in (clockwise from top left) lingual, cross-section
113 at the cemento-enamel junction, cervical third, middle third, apical third, and apical views. B.
114 Taurodont molar, apically displaced pulp chamber and canals outlined in white. C. Peg-shaped
115 root. Images A, C from the Root Canal Anatomy Project
116 <http://rootcanalanatomy.blogspot.com/> (accessed 10 March 2021). Image B from
117 <http://www.dentagama.com> (accessed 27th March 2021).
118

119 External Root morphology

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

128 Some exceptions exist. Tomes' roots [9] have a long history of study in the
129 anthropological literature, and are included in the ASUDAS. These single rooted teeth are
130 part of a morphological continuum in which the mesial surface of the root displays, in
131 varying degrees of depth, a prominent developmental groove [1]. Tomes first described this
132 root configuration in modern human mandibular premolars and classified it as a deviation

133 from the “normal” European single rooted premolar (ibid). Tomes’ root appears in 10% of
134 P₃s and P₄s of the Pecos Native American Tribe [18], 36.9% of P₃s and 8.4% for P₄s in the
135 Bantu [17], and >25% for Sub-Saharan African groups [2]. In contrast, P₃ Tomes’ roots
136 account for 0-10% of Western Eurasian populations and 10-15% of North and East Asian
137 population (ibid). In its most extreme form, the groove appears on mesial and distal surface,
138 and can result in bifurcation of the root. In cross section, Tomes’ roots have a V-shaped
139 ‘notch’ where the two radicals are dividing. Occasionally, this division results in bifid apices
140 or two separate roots, depending on the level of bifurcation [52].

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

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

153

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

158

159 **Root canals**

160

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

164

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

167

168 With exception of the anterior teeth, this is rarely the case, and there are often multiple
169 canal configurations within a single root (Fig 5). A wide range of canal configurations have
170 been reported [11,56–58], though the number of configurations vary by study. Often, these
171 discrepancies are due to the inclusion or exclusion of accessory canals (lateral and furcation
172 canals), which branch from the main canal structure, like the roots of a tree, at the point of
173 bifurcation or the apical third. However, most practitioners opt to exclude these from
174 typologies as they are not continuous structures from the pulp chamber to the root apex.
175

176 Fig 5. **Vertucci's widely used canal classification system.** Root and canal number do not
177 always conform to one another. Black area represents pulp chambers and various canal
178 configurations [56].
179

180 In conjunction with external form, canal morphology has proven useful for hominin
181 classification [59–62]. In mandibular premolars, researchers have shown that combined
182 external morphologies and canal configurations can differentiate robust and gracile
183 australopiths [61,63,64]. However, it is unclear how internal variation relates to external
184 morphology or is partitioned between and across populations.
185

186 **Canal classification systems**

187

188 The most widely used canal typology system contains eight types (Fig 5), which can,
189 theoretically, be found in any tooth in the jaws [56]. However, this classification system
190 does not include all known canal types. For example, canal isthmuses - complete or
191 incomplete connections between two round canals are frequently found in molars (Fig 6,
192 left), though they appear in other roots [58]. These canal configurations are distinct from
193 those described by Vertucci et al., [56] . Likewise, C-shaped canals have been the subject of
194 several studies [8,65,66], and their configurations are nearly identical (though ordered
195 differently) to the canal isthmuses described by Hsu and Kim [58], only stretched around an
196 180° arc (Fig 6, right). These same isthmus canal configurations can also be found in Tomes'
197 roots [67,68].
198

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

201
 202 Many classification systems have been introduced (Table 1). However, they often
 203 focus on one tooth type or morphology. Of the 27 traits catalogued by the ASUDAS, only
 204 root number for specific teeth (P^3 , M^2 , C_1 , M_1 , and M_2) and external morphology (Tomes'
 205 root) are included [1]. Others systems are only focused on the canal configurations of
 206 maxillary premolars [33], the mesial canals of mandibular 1st and 2nd molars [69], or more
 207 narrowly, unusual canal types such as isthmus [58] or C-shaped canals [11,66]. Others
 208 propose separate classificatory nomenclature based on root number[57], or maxillary [70]
 209 and mandibular molars [71].

210

211 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

212
 213 While canal number and morphology do not always conform to external number and
 214 morphology [50,55,61], the literature on the relationship between internal and external
 215 morphologies is sometimes inconsistent. For example, Vertucci *et al.* [56] categorize
 216 maxillary premolars with two separate canals as type IV (Fig 6). However, it is unclear if this
 217 classification is to be applied only to two canals encased in a single or two-rooted tooth.
 218 Canal shape can also change over time due to dentin deposition [75]. While some variation
 219 may be due to age and/or biomechanical factors, there is currently no methodology to
 220 classify these changes.

221

222 Materials and Methods

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224 CT scans

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226 Using cone-beam computed tomography (CBCT or CT), we analysed both sides of the
227 maxillary and mandibular dental arcades of individuals (n= 945) from osteological collections
228 housed at the Smithsonian National Museum of Natural History (SI), American Museum of
229 Natural History (AMNH), and the Duckworth Collection (DC) at the University of Cambridge
230 Leverhulme Centre for Human Evolutionary Studies. Full skulls of specimens from the SI and
231 AMNH were scanned by Dr. Lynn Copes [76] using a Siemens Somatom spiral scanner (70
232 μA , 110 kV, slice thickness 1.0 mm, reconstruction 0.5 mm, voxel size mm^3 :
233 $1.0 \times 1.0 \times 0.3676$). Full skulls of specimens from the DC were scanned by Professor Marta
234 Mirazón-Lahr and Dr. Frances Rivera [77] using a Siemens Somatom Definition Flash scanner
235 at Addenbrooke's Hospital, Cambridge England (80 μA , 120kV, slice thickness 0.6mm, voxel
236 size mm^3 : $0.3906 \times 0.3906 \times 0.3$). For all collections, crania and mandibles were oriented on
237 the rotation stage, with the coronal plane orthogonal to the x-ray source and detector.
238 Permission to use the scans has been granted by Dr. Copes, Professor Mirazón-Lahr and Dr.
239 Rivera. A complete list and description of individuals included in this study is listed in the S1
240 table.

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

247

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

251

252 External root morphology

253 External root morphology was assessed at the measured mid-point of the root,
254 bounded by the cemento-enamel junction (CEJ) and root apex/apices. The midpoint was
255 chosen as a point of inspection because (a) the root has extended far enough from the CEJ,
256 and in the case of multi-rooted teeth, from the neighboring roots to be structurally and

257 developmentally distinct [79]; and (b) at a point in the eruptive phase in which the adjoined
258 tooth crown is in functional occlusion [80]; and, (c) does not reflect the morphological
259 alteration common to the penetrative phase in which the apical third of the root becomes
260 roughened and/or suffers ankylosis or concrescence due to penetration of the bones of the
261 jaws [80].

262

263 **Root and canal number**

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

271

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

278

279 **Canal morphology and configuration**

280

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

285

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

288

289 To classify canal configurations, we have simplified canal configurations into five
290 categories, R-R5, that reflect canal number and account for fusion/division of canals (Fig 10).

291 These categories can be found in any tooth and are applied to single roots within the root

292 complex (e.g., 3 roots, each with a single canal, would not be designated R3, but R for each
293 canal per root).

294

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

297

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

307

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

311

312 **Anatomical descriptions**

313 Categorically, incisors are indicated by an I, canines a C, premolars with P, and
314 molars use M. Tooth numbers are labelled with super- and subscripts to differentiate the
315 teeth of the maxilla and mandible. For example, M¹ indicates the 1st maxillary molar while
316 M₁ indicates the 1st mandibular molar. Numerically, incisors are numbered either 1 or 2 for
317 central and lateral incisors respectively. Canines are marked 1 as there exists only one
318 canine in each quadrant of the jaws. Through the course of evolution, apes and old world
319 monkeys have lost the first and second premolars of their evolutionary ancestors, thus the
320 remaining 2 premolars are numbered 3 and 4 [81,82].

321 Unlike the anatomical surfaces and directions used for tooth crowns, there exists no
322 formula for tooth roots. However, classical anatomical terms – mesial, buccal, distal, lingual,
323 or combinations of (e.g., mesio-buccal), can be used to describe the location of roots and
324 canals. Additionally, we use the term axial to describe a single or centrally located canal

325 within a single-rooted tooth. Because anatomical location rather than anatomical surface is
 326 being employed, buccal replaces labial (for anterior teeth) when describing roots.

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328 Results

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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	248	I ₂	247	495
I ² CON	1	I ² CON	1	-
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	362	M ₃	278	640
M ³ CON	28	M ³ CON	25	-
Total	3,495	-	2,475	5,970

346

347

348

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

349

350 Root number

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352 In aggregate, the number of roots in teeth from our sample are between one and
 353 four (Table 3). Anterior teeth almost always having a single root, the exception being two
 354 mandibular canines, premolars between one and three roots, and molars between one and
 355 four roots. Entomolaris, or three-rooted molars, appear in 18.05 % M₁S, 1.23% of M₂S, and
 356 5.94% of M₃S, while paramolaris appears in 3.63% of M₃S.

357

358 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

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

360 En = Entomolaris, Pa = Paramolaris.

361

362 Canal number

363

364 Teeth in our study contain between one and six canals (Table 4), and it is not
 365 uncommon for a single root to contain two or more canals, especially in the molars. With
 366 the exception of I¹, all single rooted anterior teeth have a double canaled variant. Molars

367 have the most canals per tooth, with M¹s showing the most variation. With the exception of
 368 I¹, canal number exceeds root number (Table 3).

369

370 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*
<u>Maxilla</u>					<u>Mandible</u>				
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

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

372

373 **Anatomical orientation of canals in the root complex**

374

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

380

381

382

383 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*
	<u>Maxilla</u>				<u>Mandible</u>		
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		

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

386

387 External root morphology at midpoint

388

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

393

394

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

398

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

403

404 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 an egg. However, a consistent feature are their 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]

405

406 External root morphologies appear in different frequencies in each tooth, and some
 407 morphologies do not appear in some teeth at all (Table 7). The number of morphologies
 408 increase posteriorly along the tooth row, and M₁s have the most morphologies. Part of this
 409 is due to the number of bifid (Bi) variants (e.g., EBi, PBi, etc.), as well as the presence of
 410 pegged and fused roots (Tables 8 and 9, respectively).

411

412 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*
<u>Maxilla</u>				<u>Mandible</u>			
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	120	48.39	I ₂	E	7	2.83
	G	25	10.08		H	1	0.40
	P	97	39.11		K	10	4.05
	W	6	2.42		P	219	88.66
C ¹	W	6	2.42	W	10	4.05	
	E	149	36.70	C ₁	E	54	18.18
	EBi [†]	1	0.25	G	6	2.02	
	G	4	0.99	H	6	2.02	
	P	135	33.25	K	2	0.67	
	W	117	28.83	P	141	47.47	
P ³	W	117	28.83	W	87	29.29	
	E	10	1.35	WBi	1	0.34	
	G	402	54.40	P ₃	E	62	17.97
	H	80	10.83	G	14	4.06	
	HBi	40	5.41	H	1	0.29	
	K	38	5.14	K	3	0.87	
	KBi	5	0.68	P	145	42.03	
	P	143	19.35	T	75	21.74	
	PBi	12	1.62	TBi	8	2.32	
W	9	1.22	W	37	10.72		
P ⁴	W	9	1.22	P ₄	E	122	38.98
	E	24	4.53	G	21	6.71	
	G	106	20.00	HBi	1	0.32	
	H	70	13.21	K	1	0.32	
	HBi	21	3.96	P	155	49.52	
	K	31	5.85	T	9	2.88	
	KBi	3	0.57	TBi	1	0.32	
	P	266	50.19	W	3	0.96	
	PBi	4	0.75				
W	4	0.75					
M ¹	W	4	0.75	M ₁	E	20	2.24
	E	500	24.27	G	76	8.50	
	G	266	12.91	H	188	21.03	
	H	11	0.53	HBi	61	6.82	
	K	49	2.38	K	73	8.17	
	P	668	32.43	KBi	4	0.45	
	PBi	4	0.19	P	437	48.88	
	W	536	26.02	PBi	17	1.90	
	WBi	2	0.09	W	18	2.01	
M ²	WBi	2	0.09	M ₂	CS	33	4.54
	E	451	28.89	CSBi	1	0.14	
	G	371	23.76	E	33	4.54	
	H	9	0.58	G	15	2.06	
	HBi	2	0.13	H	143	19.67	
	K	80	5.12	HBi	17	2.34	
	KBi	1	0.06	K	206	28.34	
	P	262	16.78	KBi	4	0.55	
	W	241	15.43	P	256	35.21	
				PBi	5	0.69	
			W	1	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

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

414

415 Pegged (Mi) roots while globular in cross section, are their considered their own
 416 distinct morphology as they are a form of microdontia [85]. They are relatively rare in our
 417 sample and only appear in M³ and M₃ (Table 8).

418

419 Table 8: Type and number of teeth with pegged roots

Tooth	External morphology	n	% of roots*	Tooth	External morphology	n	% of roots*
<u>Maxilla</u>				<u>Mandible</u>			
M ³	Mi	5	0.60	M ₃	Mi	6	1.07

420 * from Table 3

421

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

425

426 Table 9: Type and number of roots showing fusion morphologies

Tooth	External morphology	n	% of roots*	Tooth	External morphology	n	% of roots*
<u>Maxilla</u>				<u>Mandible</u>			
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				

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

430

431 Canal shape and configuration

432

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

439

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

Tooth	Canal morphology	n~	% of canalst	Tooth	Canal morphology	n~	# of canalst
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
P⁴	O	193	27.26	P₄	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				
M¹	O	357	14.69	M₁	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
M²	O	284	14.87	M₂	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
M³	O	120	11.27	M₃	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

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

444

445 **Classification system**

446

447 As discussed in the literature review above, the categorization of roots and canals
 448 can be misleading or inaccurate when systems limited to tooth/canal type are applied to
 449 other root/canal types. Problematically, classification scheme exists that captures all
 450 components of the complete tooth root phenotype. We have presented here a new system
 451 that is simple, accurate, human and computer readable, and allows for easy qualitative

452 and/or quantitative analysis of the entire phenotype, or each of its constituent parts,
453 individually or in any combination. We have outlined five phenotypic elements (E) that
454 comprise the human tooth root phenotype: E1 - root number, E2 - canal number, E3 – canal
455 location, E4 - external morphology, and E5 – canal morphology and configuration. The
456 system provides codes for each element, and the resulting combination constitutes that
457 root complex's complete phenotype code.

458

459 **Tooth name or number**

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

464

465 **Root number or absence**

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

473

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

476

477 **Canal number**

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

483

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

485

486 **Anatomical locations of canals**

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

493

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

498

499 **External Root Morphology**

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

510

511 Fig 16. **Flow chart for determining and recording phenotype element 4 - external root**
512 **morphology.**

513 *if root is bifurcated, append morphology with Bi. Ex: P = plate, PBi = plate-bifurcated. Right:
514 axial CT slices showing external root morphologies.

515

516

517 **Canal configuration**

518

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

522

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

529

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

533

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

538

539

540 **Fig 19. Five phenotypic elements of a lower left 1st mandibular molar (RM₁-R2-C3-M2D1-**
541 **MHDP-MR2DO).** A. E1 - Root presence/absence; B. E2 - Canal presence/absence, C. E3 -
542 Canal location, D. E4 - Canal morphology, E. E5 - Canal shape. Images A and B from the Root
543 Canal Anatomy Project <https://rootcanalanatomy.blogspot.com/> (accessed 10 March 2021)

544

545

546

547 **Redundancy of information**

548

549 There is a bit of redundancy of information in our system. For example, R2-C3-
550 M2D1-MHDP-MR2DO can be shortened to MHR2-DPO without loss of information. MHR2
551 describes a mesial (M) root (1 root) that is hourglass (H) shaped with two round (R2) canals
552 (C), while DPO describes a distal (D) root (1 root) that is plate (P) shaped, with one ovoid (O)
553 canal (C). However, there are several issues with this shorter version. The first is that we
554 designed to our system to record phenotype elements individually or in combination. MHR2

555 describes what is potentially a single rooted tooth or could be a four rooted tooth. R2
556 indicates that the root complex is two-rooted, as does M2D1, MHDP, and/or MR2DO. The
557 second is human and computer readability. For a human, R2-C3-M2D1-MHDP-MR2DO is
558 easier to read and understand than MHR2-DPO. For a computer, R2-C3-M2D1-MHDP-
559 MR2DO allows easy separation and/or recombination of elements for analysis. The third is
560 that not all users will have visual access to all elements within a root complex. It might be
561 lack of equipment (radiography) or missing teeth. Thus, our system is also designed to
562 capture the most information available to the user, missing information can be easily
563 represented. Although there is a level of redundancy, the system is optimized for human
564 and machine reading.

565 **The phenotypic set within the morphospace of root diversity**

566
567 Within these phenotypic elements, there is exist 841 unique phenotype element
568 permutations derived from our global sample. These comprise our study's "phenotypic set"
569 among the range of potential phenotypic permutations. Anterior teeth have the least
570 number of permutations while molars, particularly maxillary molars, have the greatest (Fig.
571 20).

572
573 Fig 20. **Number of phenotypes in individual teeth.**

574

575 **Discussion**

576
577 This paper set out to present a method that would capture quantitatively and
578 qualitatively the diversity of human tooth root phenotypes, using a modular approach. It has
579 shown that it is possible to have a universal code for phenotyping roots, and that a global
580 sample of modern humans demonstrates the high level of tooth root phenotype diversity. A
581 more comprehensive set of tooth root data should reinforce and expand the broader toolset
582 for studying human phenotypic diversity (e.g., tooth crowns, craniofacial morphometrics,
583 genetics, etc.).

584 The large number of phenotypes permutations found in our sample can be explained
585 by the variation within each element. For example, Table 10 shows how permutations in
586 one element can result in four nearly identical tooth roots with four different phenotype
587 codes. Here, all these roots are identical in their phenotypic elements with the exception of

588 their external morphology (E4). Teeth with more roots result in a greater number of
589 permutations. Fig 21 illustrates how increasing numbers and multiple combinations, and
590 orientations of root morphologies create the morphological permutations of the external
591 phenotypic elements. However, compared to tooth crowns, the number of phenotype
592 permutations is relatively few, as a recent test of ASUDAS crown traits indicates greater
593 than 1.4 million combinations, or permutations of crown phenotypes [88].

594

595 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

596

597

598

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

603

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

619 case for fossil hominins, more regular scanning of more recent samples will be essential for
620 studies of human diversity.

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

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

647 Finally, for the method to be worthwhile, it is necessary for it to be useful in relation
648 to current hypotheses and research foci. Four are immediately apparent. First, current
649 interest in the role of dispersals, not just the initial one from Africa [98–100], but also the
650 increasing genetic evidence for multiple later regional dispersals means that finding ways of

651 linking the palaeoanthropological and archaeological record to the inferred genotypes
652 requires diverse phenotypes, and methods such as this will be required [101–104]. The
653 second is in terms of earlier phases of human evolution; with the current evidence for
654 interbreeding across hominin taxa [105], it is necessary to have appropriate phenotypic
655 systems – and roots are likely to be a good one – to tease out the phenotypic effects in such
656 admixture [106,107]. Third, there is considerable interest in modularity and integration in
657 evolution, and the modular approach adopted here may provide a suitable model system
658 for exploring these issues [108,109]. And finally, biomechanical and spatial studies of the
659 hominid masticatory system can draw quantitative functional and dietary inferences from
660 root and canal number and morphology [110–113].

661

662 **Conclusions**

663

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

675

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679

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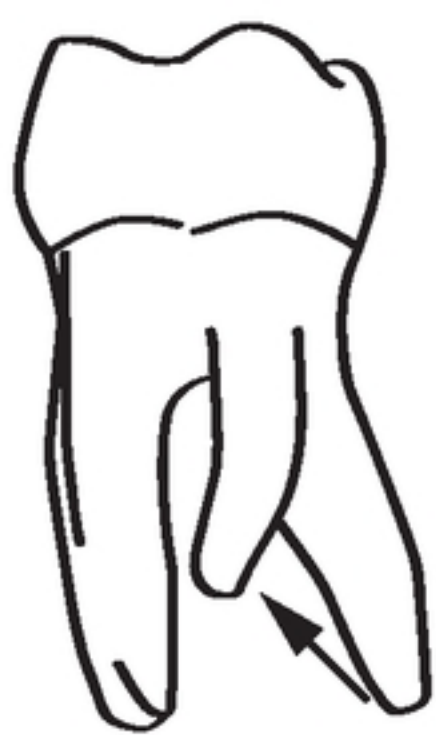
992 **Supporting information**

993

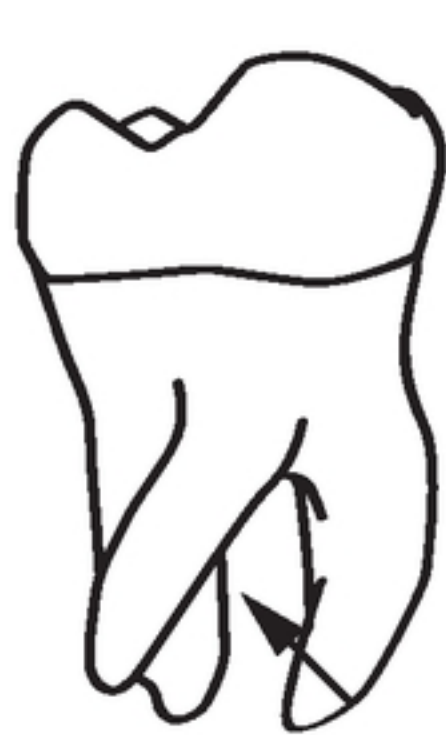
994 See S1 Table



A1



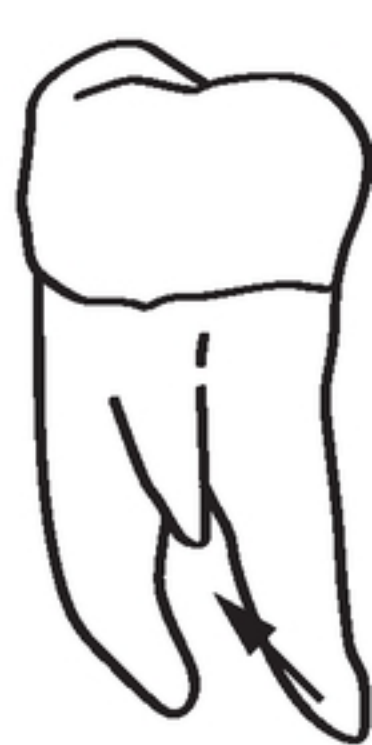
A2



B



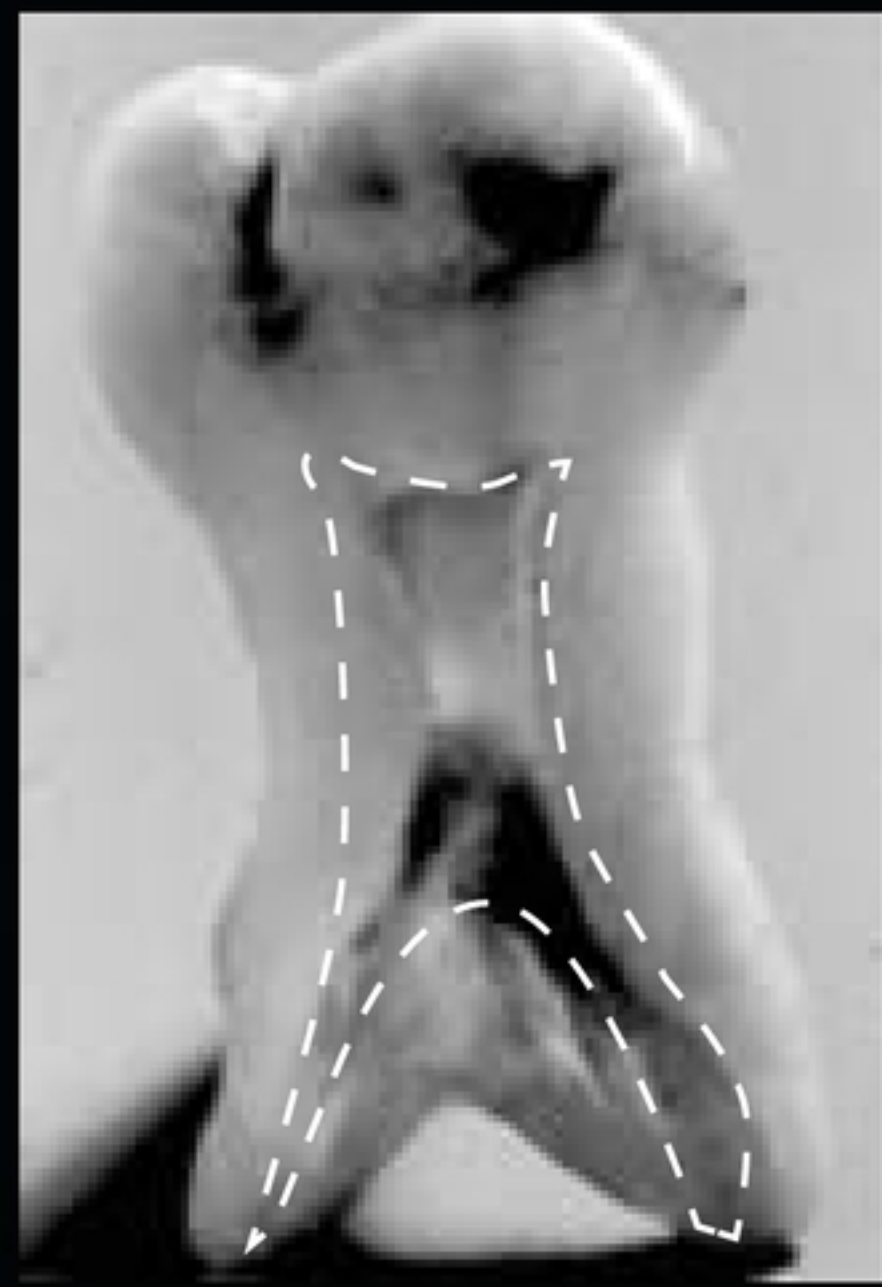
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D



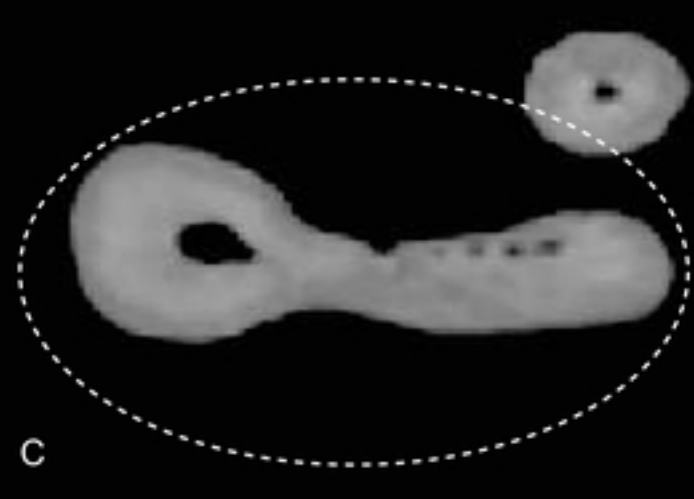
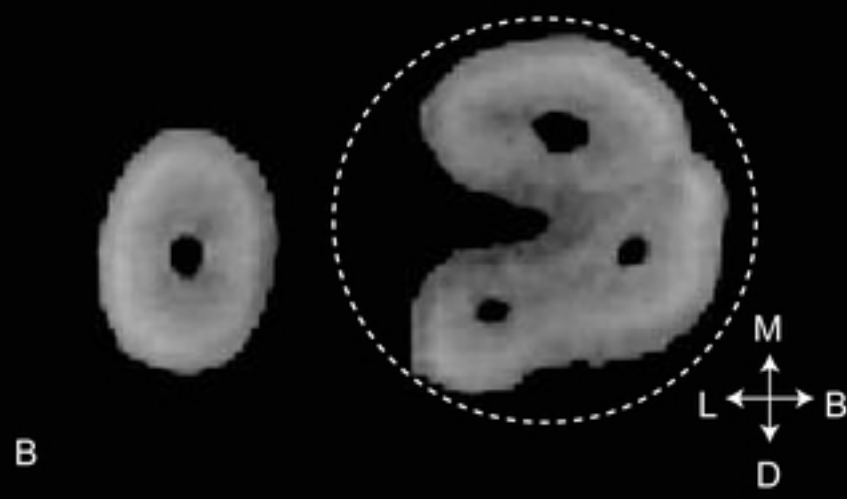
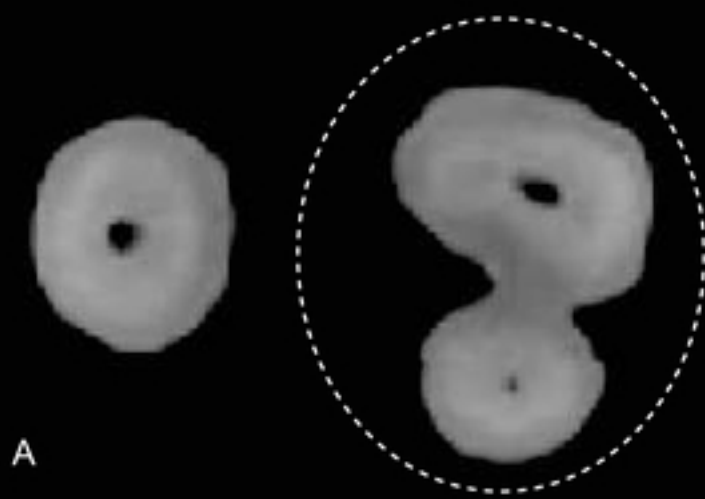
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Type 1

Type 2

Type 3

Type 4

Type 5

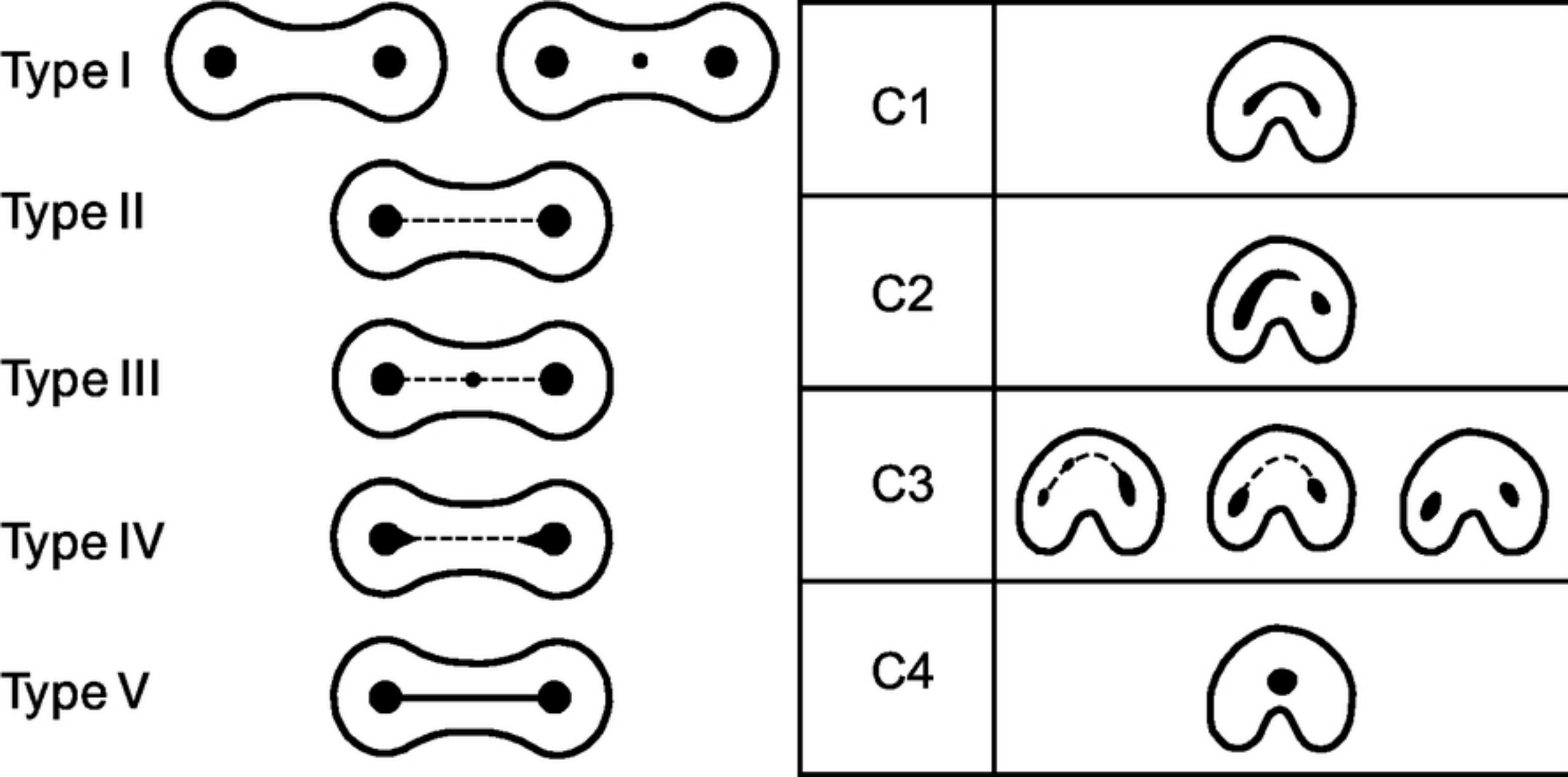
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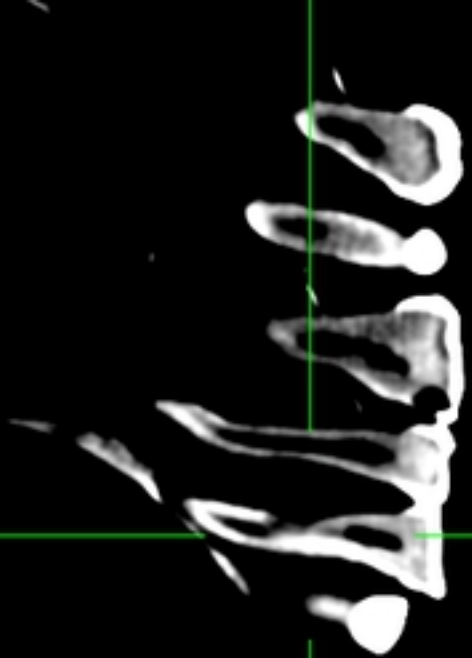
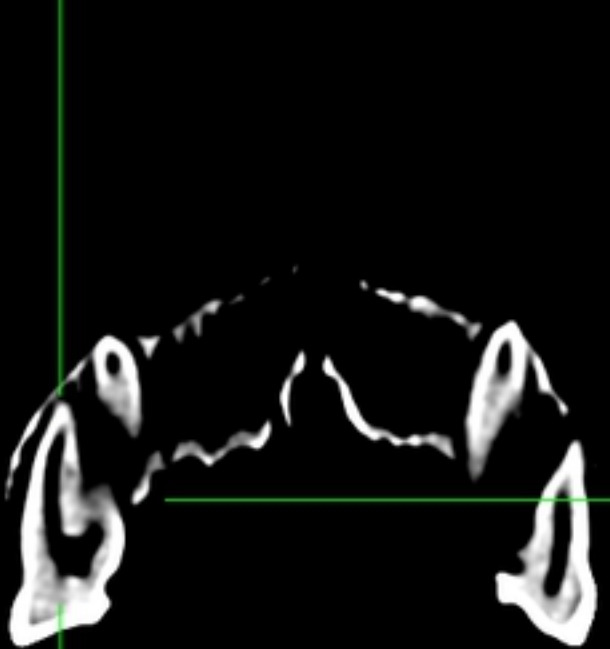
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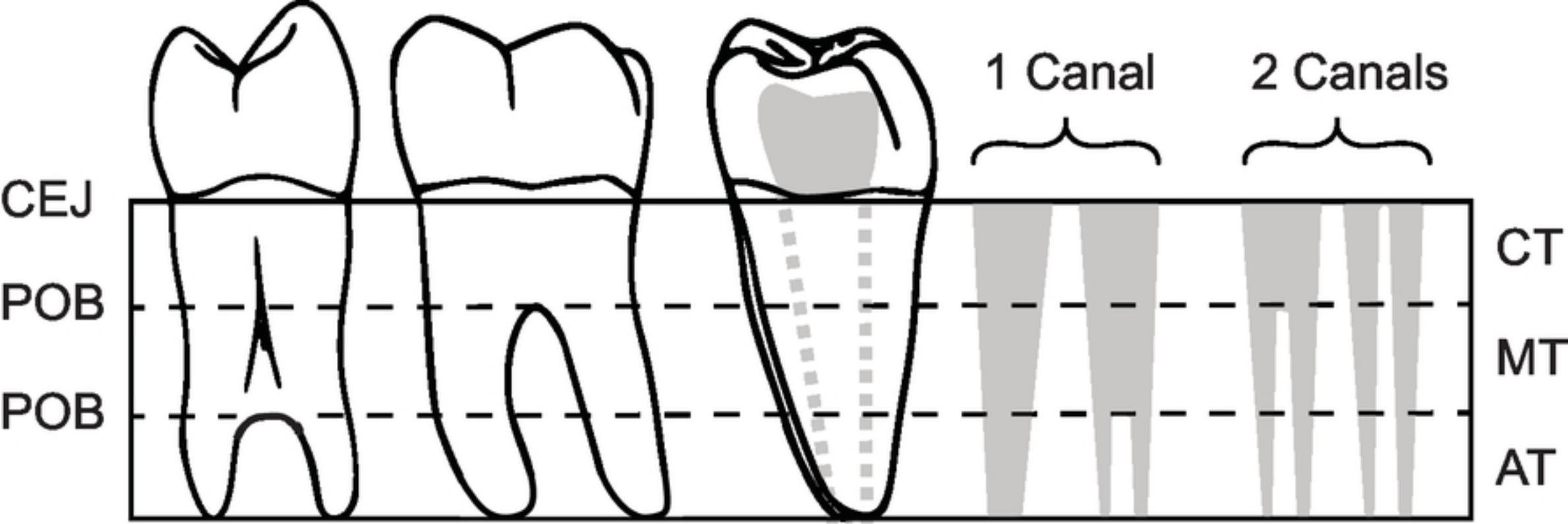
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R



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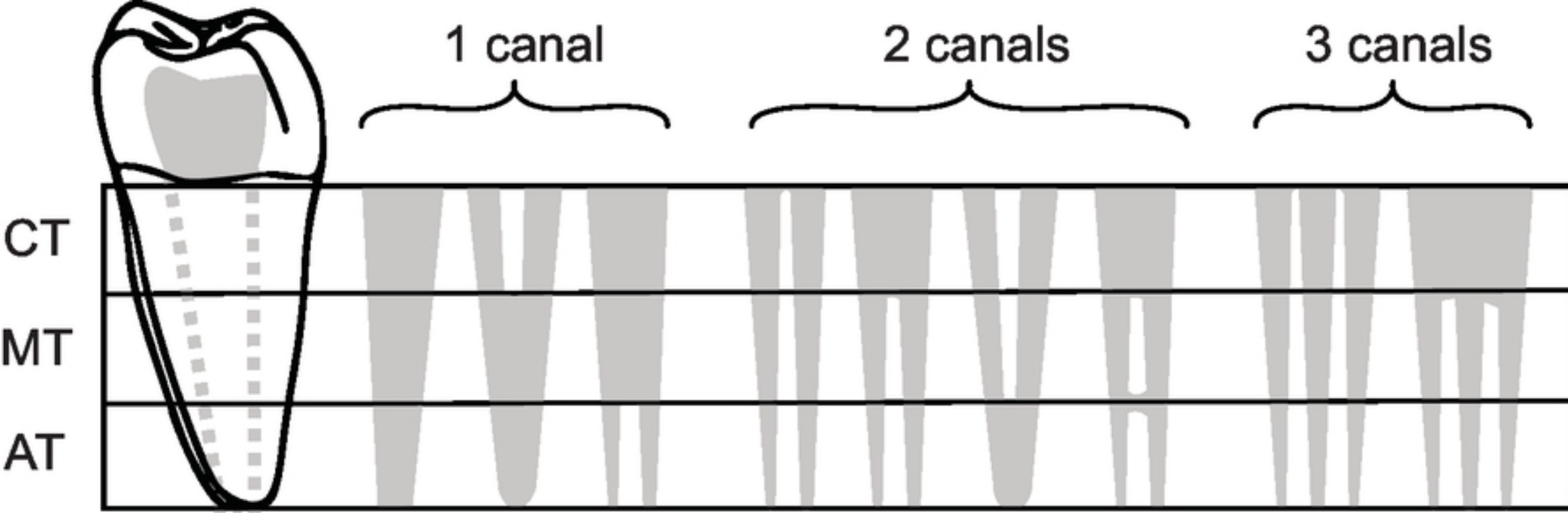


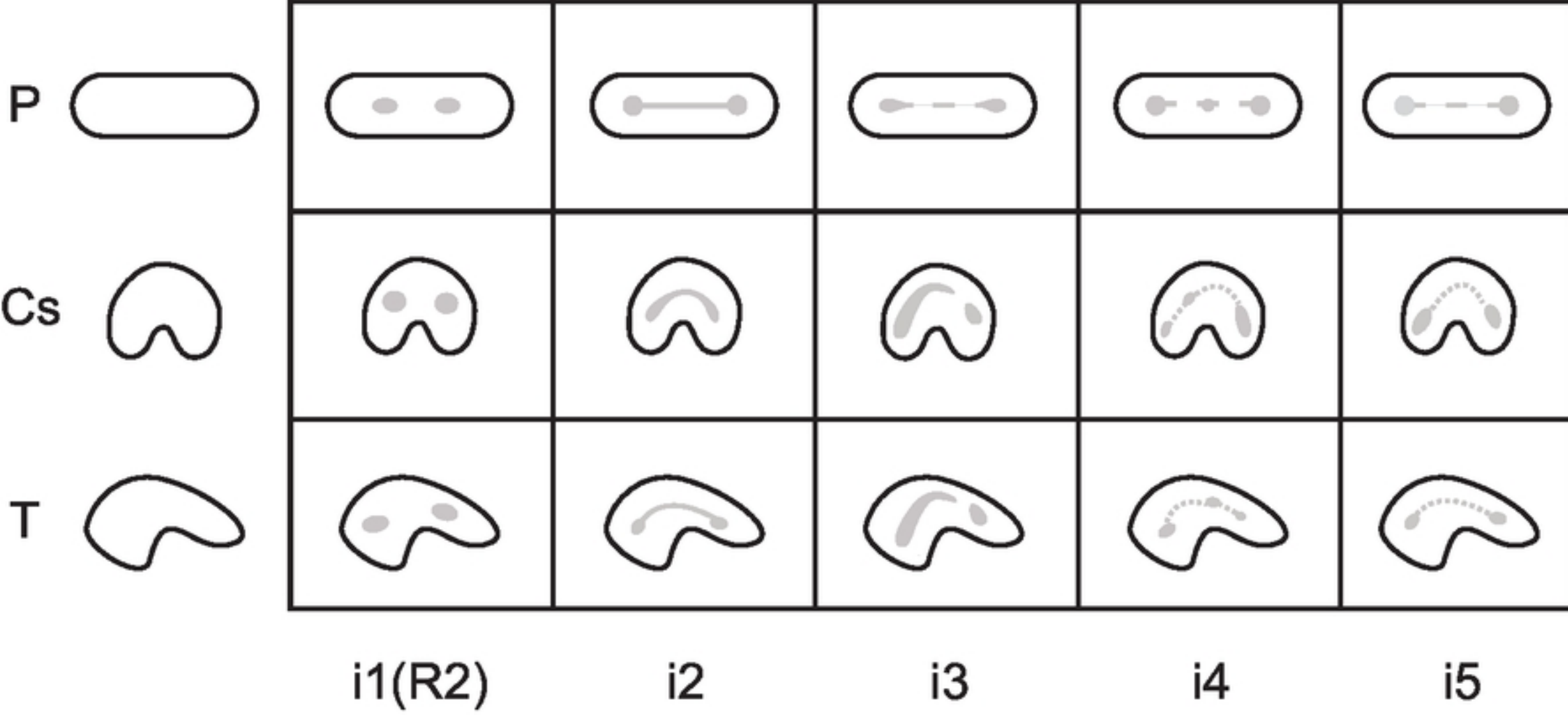
R2

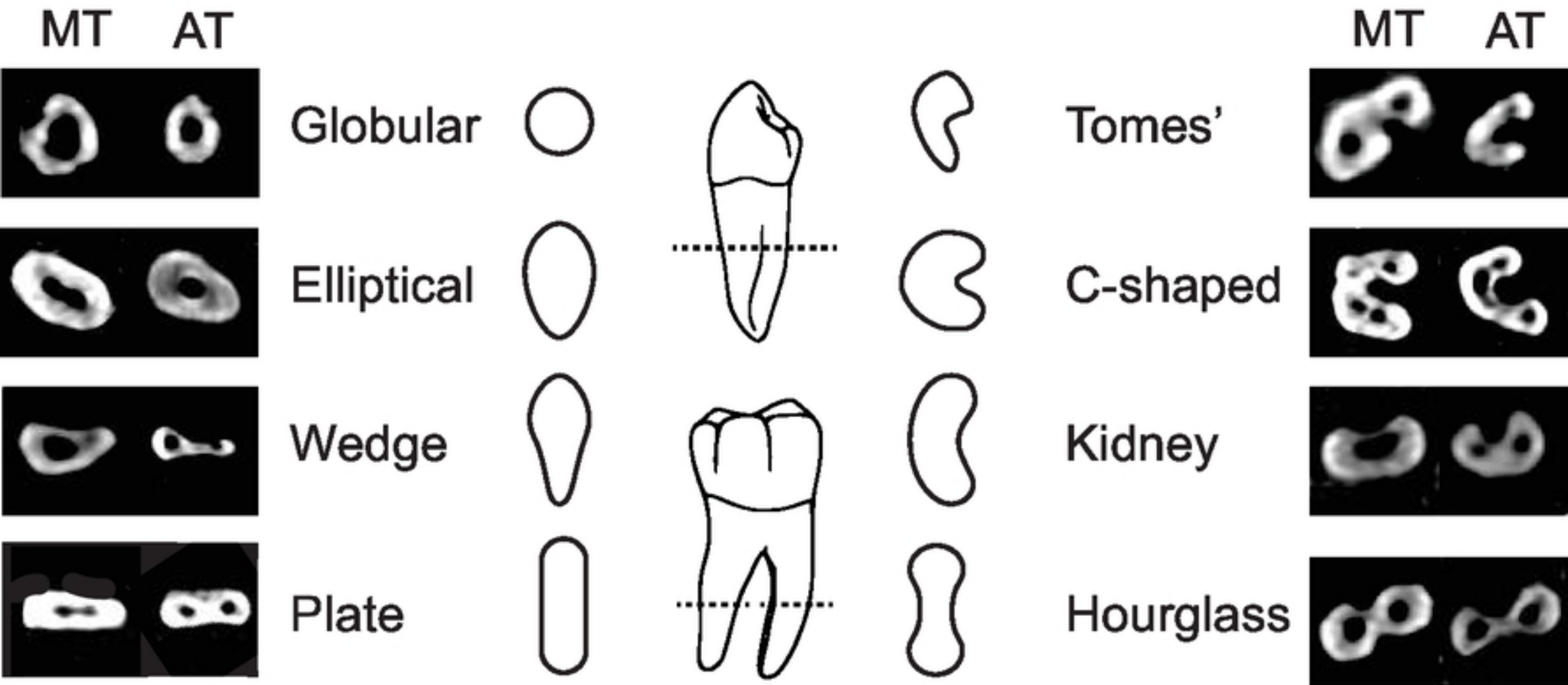


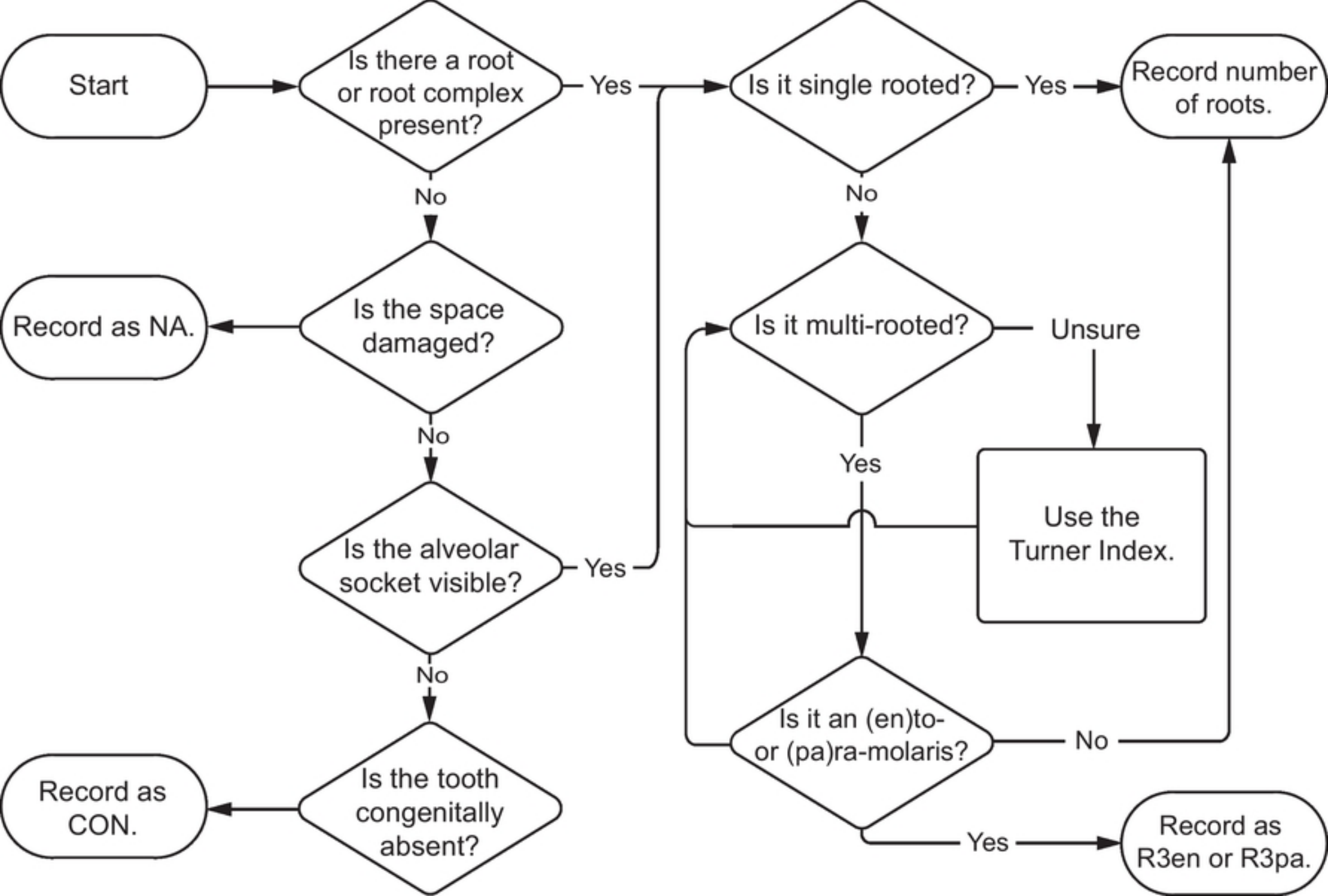
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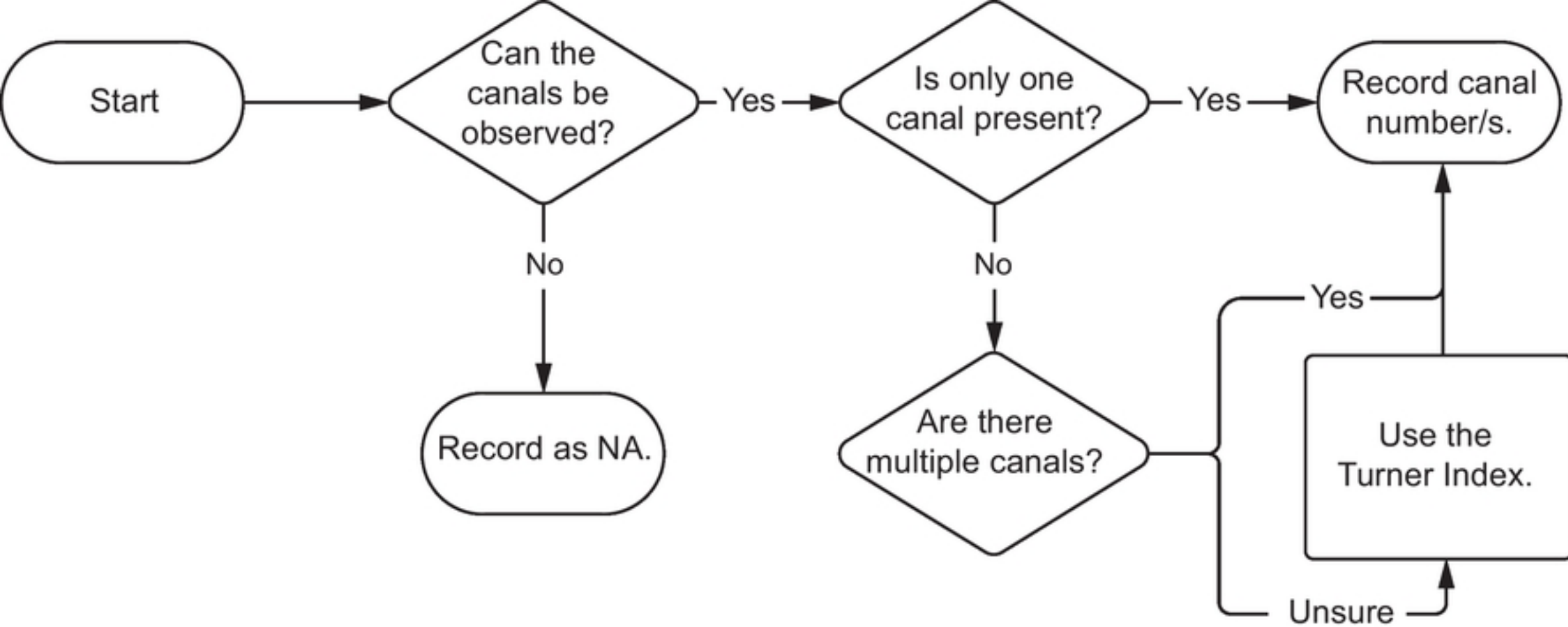


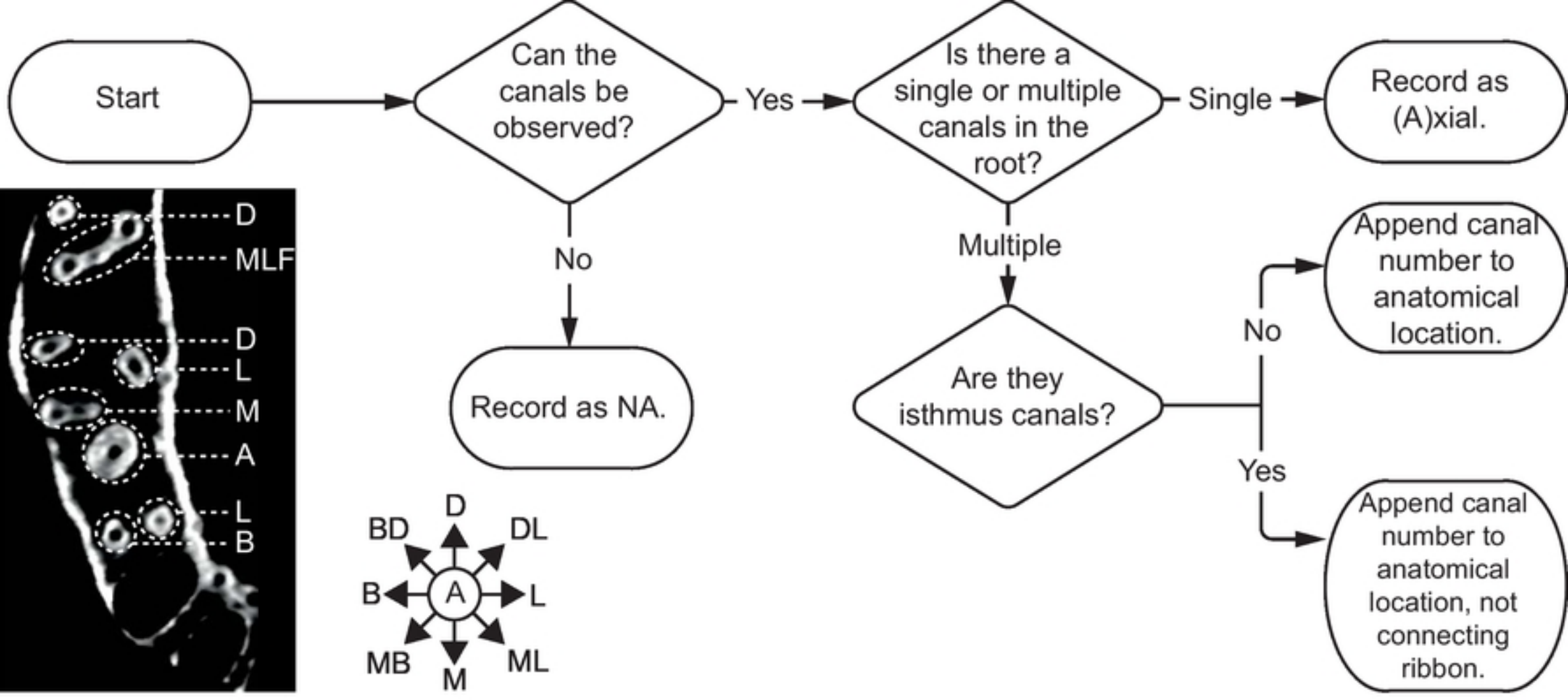


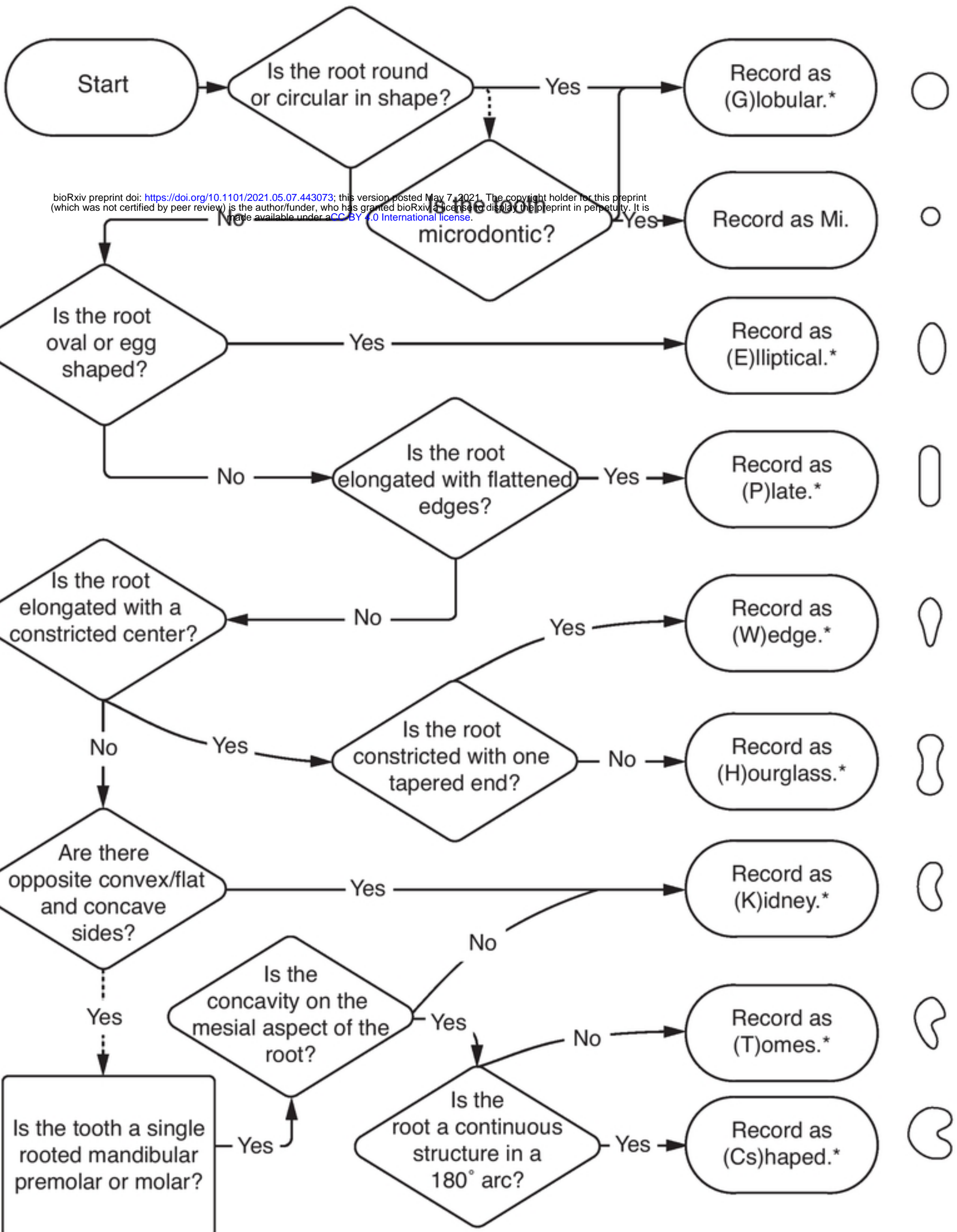


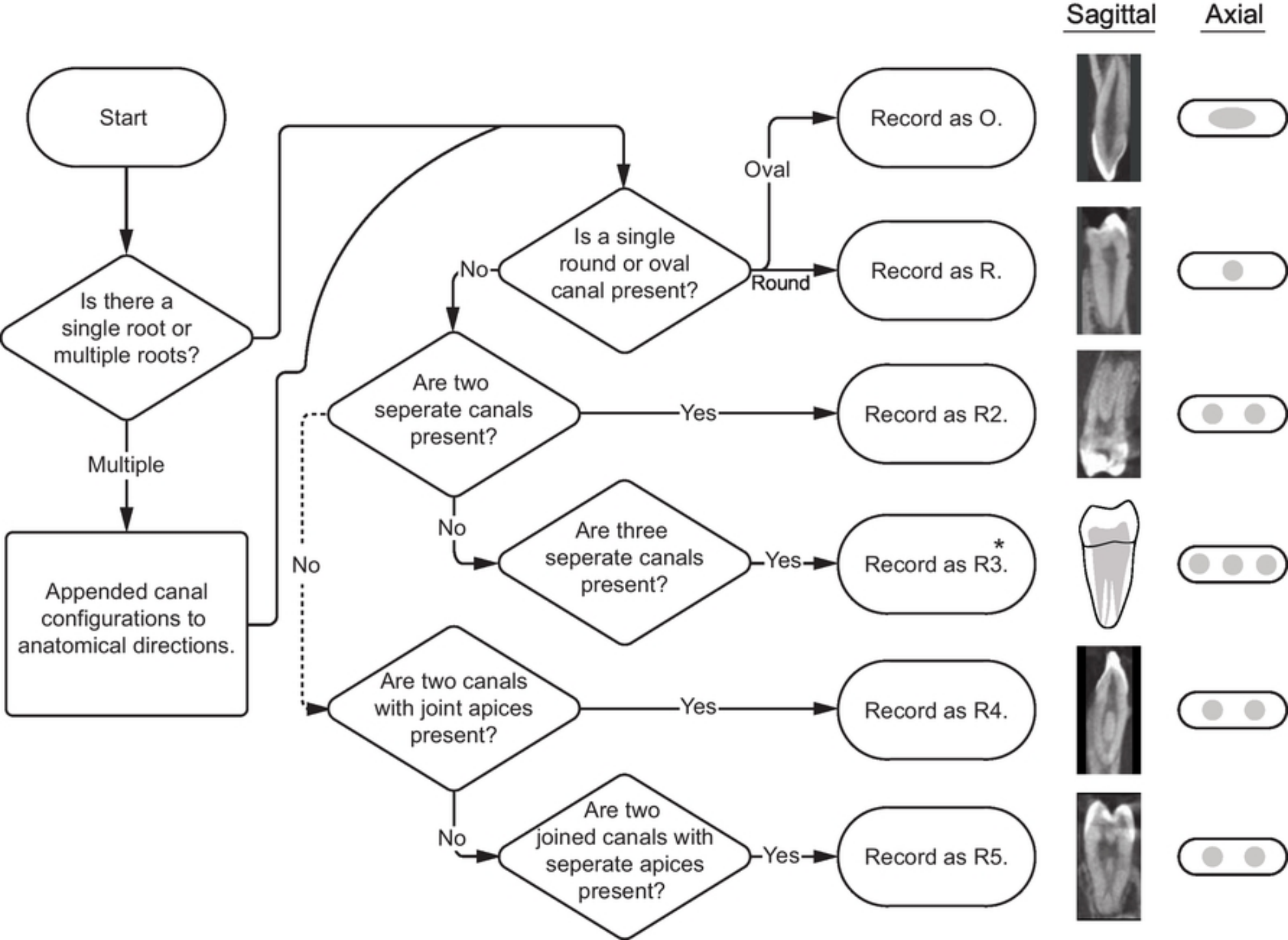


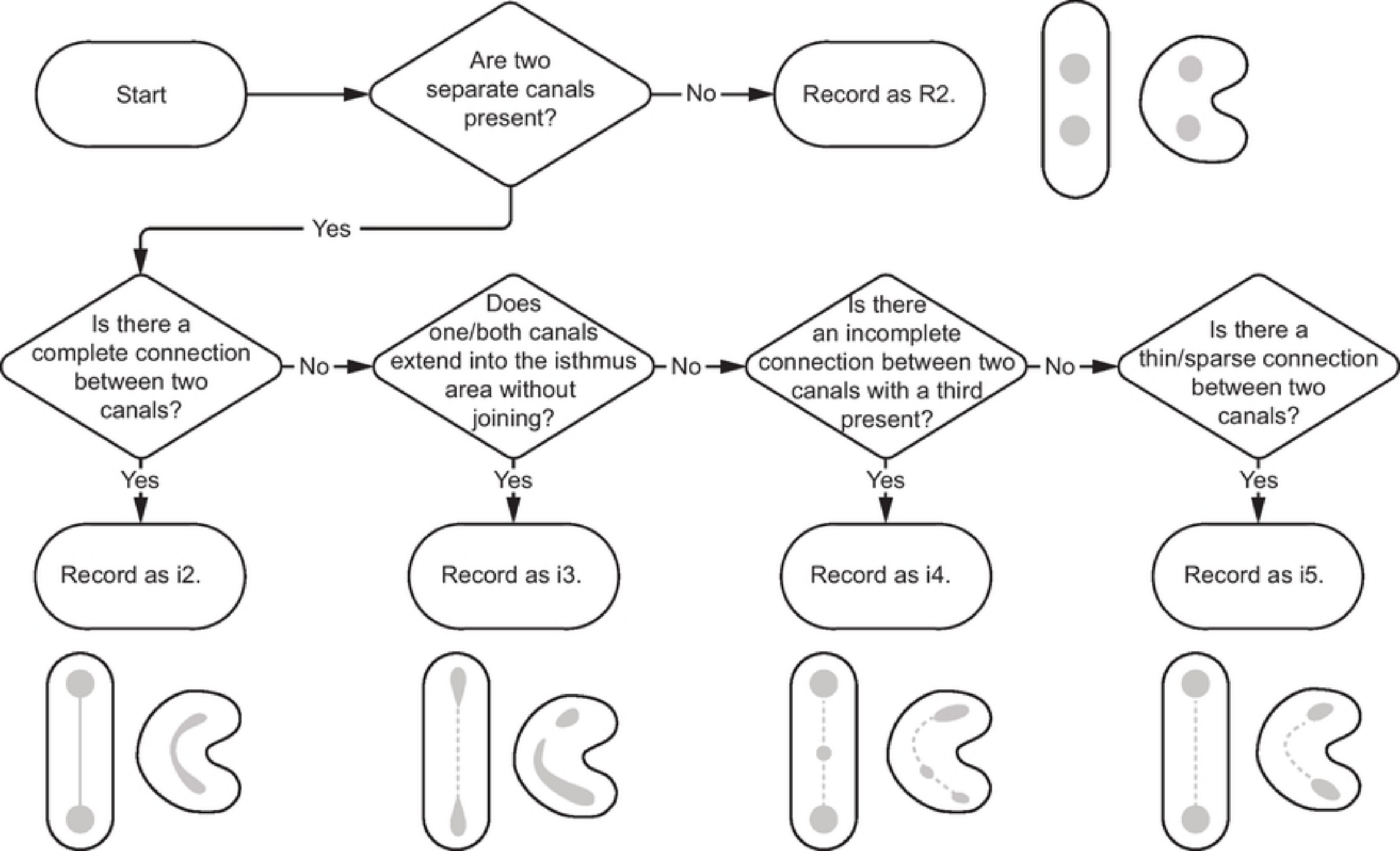












A



B



C



D



E



