

THE OLDEST SPECIES OF *DOLICHOTIS* (RODENTIA, HYSTRICOGNATHI) FROM THE  
PLIOCENE OF ARGENTINA: REDESCRIPTION AND TAXONOMIC STATUS OF

*ORTHOMYCTERA CHAPALMALENSE*

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**Morphological Character List and GenBank accession numbers.**

**Characters with an asterisk (\*) are considered ‘ordered’.**

**Mandibular characters**

1. Mental foramen: absent (0); present (1).
2. \*Location of the mental foramen on the anterior region of the dentary: dorsal on the diastema (0); close to the dorsal margin of the dentary and opening dorso-laterally (1); at the dorso-ventral midpoint of the lateral surface of the dentary and opening laterally (2); close to the ventral margin of the dentary and opening laterally (3).
3. Dorso-ventral position of the mandibular foramen respect to the retromolar fossa: dorsal (0); ventral (1).
4. \*Antero-posterior position of the mandibular foramen respect to the retromolar fossa, when the mandibular foramen is ventral to it: posterior (0); at the same level (1); anterior (below m3) (2).
5. Posteroventral projection of the posterior end of the mandibular symphysis (“chin”), in lateral view: absent (0); present (1).
6. Development of posteroventral projection of the posterior end of the mandibular symphysis (“chin”), in lateral view: well developed, forming an elongate peg exposed in lateral view (0); moderately developed, only a low bulge projects ventrally and is marginally exposed in lateral view (1).
7. Labial edge of the condyle that is the insertion point of *m. masseter posterior*, in posterior view: projecting laterally with respect to wall of the dentary, forming a small knob (0); lacking a distinct knob, continuous with lateral wall of the dentary (1).

8. Medial edge of the condyle that is the insertion point of *m. pterygoideus externus*, in posterior view: projecting medially forming a shelf that overhangs the medial surface of the dentary (0); poorly developed projecting medially forming a small knob with respect to medial wall of the dentary (1).
9. Shape of the post-condylar process, in lateral view: squared-off, forming approximately a right angle (0); rounded (1).
10. Length of the post-condylar process: equal to or longer than the antero-posterior length of the condyle (0); shorter than antero-posterior length of the condyle (1).
11. Height of the coronoid process compared to the position of the condyle: located at the same dorso-ventral level as the condyle (0); located more ventrally than the condyle (1).
12. \*Anterior margin of the coronoid process: convex (0); straight (1); concave (2).
13. Dorsal end of the coronoid process: pointed and postero-dorsally projected (0); pointed and dorsally projected (1); blunt (2).
14. \*Dorso-ventral position of the mandibular notch: located above the occlusal surface of the dental series (0); located at the same height as the occlusal surface of the dental series (1); located ventral to the occlusal surface of the dental series (2).
15. Shape of the mandibular notch: concave (0); almost straight (1).
16. \*Dorso-ventral position of the anteriormost point of the lunar notch: low, located ventral to the dorso-ventral midpoint of the dentary (between the ventral edge of the dentary and the condyle) (0); located at the approximate dorso-ventral midpoint of the dentary (1); high, located above the dorso-ventral midpoint of the dentary (2).
17. Posterior extension of the angular process: level with the post-condylar process (0); ending anterior to the post-condylar process (1); ending posterior to the post-condylar process (2).
18. \*Pterygoid shelf: developed (0); reduced (1); absent (2).
19. Mylohioid shelf: absent (0); present (1).
20. \*Posterior extension of the root of the lower incisors: extending up to the level of m3 (0); extending up to the level of the posterior lobe of m2 (1); extending up to the level of the anterior lobe of m2 (2); extending up to the level of the posterior lobe of m1 (3); extending up to the level of the anterior lobe of m1 (4).
21. \*Location of the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis* with respect to the tooth row: between p4 and m1 (0); below m1 (1); between m1 and m2 (2).
22. Ridge of the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*: absent (0); present (1).

23. \*Development of the ridge of the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*: poorly developed (0); developed, without forming a shelf around the notch (1); well developed, forming a shelf around the notch (2).
24. \*Notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis*: connected to the masseteric crest (0); isolated, located between the masseteric crest and the horizontal crest (1); connected to the horizontal crest (2).
25. \*Development of the masseteric crest: well developed, forming a shelf that projects laterally with respect to the lateral surface of the dentary (0); forming a well-developed ridge that fails to project with respect to the lateral surface of the dentary (1); poorly developed as a thin and low ridge (2); forming a scar (3).
26. Dorso-ventral length of the masseteric scar: high (0); low (1).
27. \*Anterior origin of the masseteric crest with respect to the tooth row: below m1 (0); between m1 and m2 (1); below m2 (2); between m2 and m3 (3); below m3 or posteriorly to m3 (4).
28. Shape of the lateral crest (*sensu* Woods 1972): straight, projecting antero-ventrally from the base of the coronoid process (0); curved, deflecting anteroventrally from the base of the coronoid process (1).
29. Horizontal crest: absent (0); present (1).
30. \*Development of the horizontal crest: present as a low and broad ridge (0); present as a conspicuous crest, forming a laterally projected shelf but lacking a dorsal fossa (1); well developed, forming a laterally projected shelf and bearing a fossa on its dorsal surface (2).
31. \*Posterior extension of the horizontal crest, in lateral view: extending up to the anterior margin of the mandibular condyle (0); approximately ending at the antero-posterior midpoint of the mandibular condyle (1); extending up to the posterior margin of the mandibular condyle (2).
32. Depth of the fossa located dorsal to the horizontal crest with respect to the dorso-ventral depth of the notch for the insertion of the tendon of the *m. masseter medialis pars infraorbitalis* when the nMpi is joined to the horizontal crest: notch and fossa different in depth (0); notch and fossa equal in depth (1).
33. Alveolar protuberance of the m1 (ventral outgrowth of the base of some molariform alveoli that projects ventrally from the ventral surface of the dentary): absent (0); present (1).
34. Development of alveolar protuberance of m1: present as a small but distinct convexity on the ventral margin of the dentary (0); present as well-developed bulge on the ventral margin of the dentary (1).

35. Antero-posterior length of the lower diastema respect to the molariform series: equal or shorter than molariform series (0); longer than the molariform series (1).
36. Dorsal margin of the lower diastema: oblique (0); subplane (1).

### **Cranial characters**

37. Anterior extension of the lateral margin of the nasal with respect to premaxilla: it extends along the entire premaxilla (0); it does not extend along the entire premaxilla (1). (Modified from Cerdeño et al., 2019).
38. Proportion of the anterior extension of the lateral margin of the nasal when it does not extend along the entire premaxilla: more than 60% (0); less than 60% (1). (new character).
39. \*Posterior extension of dorsal process of the premaxilla: anterior to P4 (0); at the same level of P4 (1); posterior to P4 (2)
40. Interorbital width (relationship between the narrower width of the frontals in the orbit and the largest width of the braincase posterior to the zygomatic squamosal process): long (> 50%) (0); short (<50%) (1).
41. Posterior portion of the frontals: plane (0); convex (1).
42. \*Anterior portion of the parietals: plane (0); slightly convex (1); strongly convex (2).
43. Interparietal in adult specimens: present (0); absent (1).
44. \*Proportion of supraoccipital in dorsal view, respect to the antero-posterior length measured from the fronto-parietal suture up to posterior margin of supraoccipital: up to 9% (0); between 9.1% and 20% (1); more than 20% (2).
45. Area between temporal fossae: plane interposed (fossae do not merge on the middle line) (0); sagittal crest (1).
46. Development of the temporal fossae: shallow (0); intermediate (1); deep (2)
47. Antero-posterior length of the upper diastema respect to molariform series: equal or longer than the molariform series (0); shorter than molariform series (1).
48. Nasolachrial foramen: laterally open (0); closed (1).
49. Depth of the masseteric fossa on the rostrum: shallow (0); deep (1).
50. Ridge through which the maxillary artery and the infraorbital nerve pass (Cherem and Ferigolo, 2012): absent (0); present (1).
51. Development of the ridge through which the maxillary artery and the infraorbital nerve pass: reduced (0); developed (1); very developed (2).
52. Dorsal process of the zygomatic squamosal process: absent (0); present (1).
53. Position of the boundary between the mastoid and paraoccipital processes: at the same level or above the external auditory meatus (0); beneath the external auditory meatus (1).

54. Dorso-ventral position of the external auditory meatus respect to the occlusal surface of the dental series (lateral view): at the same level (0); below the occlusal surface of the dental series (1).
55. Posterior border of the upper diastema: oblique (0); vertical (1).
56. \*Posterior border of the upper diastema (length from posterior border of incisor foramen to alveolus P4) respect to the antero-posterior length of maxilla (measured from the premaxillary-maxillary suture to the posterior border of maxilla at level of the posterior projection of M3): up to 10% (0); between 10.1% and 13% (1); between 13.1% and 16% (2); between 16.1% and 20% (3); more than 20% (4).
57. Length of incisive foramina (relationship between the antero-posterior length of the incisive foramina and the antero-posterior length of the diastema –from the posterior margin of the incisor alveolus to the most anterior margin of the alveolus of p4): long (>50%) (0); short (50%) (1).
58. Maximum width of the posterior margin of the incisive foramina respect to the maximum width of maxilla at same level: narrow (< 50%) (0); wide ( $\geq$  50%) (1).
59. Palatal surface: plane (0); only anterior portion concave (1); concave (2); uneven (3)
60. \*Location of the apex of the mesopterygoid fossa with molar series, when the M3 has one or two lobes: level with the M2 (0); between M2 and M3 (1); level with the M3 (2).
61. \*Location of the apex of the mesopterygoid fossa with molar series, when the M3 has three or more lobes: level with the anterior portion of the M3 (0); level at the middle point of the M3 (1); level with the posterior portion of the M3 (2).
62. Shape of the apex of mesopterygoid fossa: acuminate (0); curved (1); blunt (2).
63. Margins of the mesopterygoid fossa: convergent (0); subparallel (1).
64. \*Maximum length of bullae (antero-medial/postero-lateral) respect to antero-posterior length from the premaxillary-maxillary suture up to anterior border of magnum foramen: up to 20% (0); between 20.1% and 25 % (1); between 25.1% and 34% (2); more than 34% (3).
65. \*Maximum width of the anterior half of the basioccipital respect to width of the basicranium at the same level: up to 20% (0); between 20.1% and 30% (1); between 30.1% and 40% (2); more than 40% (3).

### **Dental characters**

66. \*Degree of hypsodonty: slightly hypsodont, having the root and the antero-posterior length of the occlusal surface longer than the height of the crown (0); mesodont, having the root and the antero-posterior length of the occlusal surface approximately equal to the height of the crown (1); protohypsodont, having the root and the antero-posterior length

of the occlusal surface less than half the height of the crown (2); euhypsodont, lacking roots (3).

67. Cement in late ontogenetic stages: absent (0); present (1).
68. Cement in young-adult ontogenetic stages: absent (0); present (1).
69. Cement in juvenile ontogenetic stages: absent (0); present (1).
70. Fossettes/ids in late ontogenetic stages: present (0); absent (1).
71. Fossettes/ids in young-adult ontogenetic stages: present (0); absent (1).
72. Fossettes/ids in juvenile ontogenetic stages: present (0); absent (1).
73. Mesofossettoid in young-adult stages: present (0); absent (1).
74. Distribution of enamel in molars: covering the entire crown (0); interrupted at the base of the lingual wall (1); interrupted at the base and the corner of the lingual wall (2); interrupted at the base and in two strips (3); interrupted along the entire labial wall of the upper molars (lingual of the lower molars) except for the flexus/id opposite to the hypoflexus/id (4); interrupted along the entire lingual wall and antero-lingual and postero-lingual walls (5).
75. Position of upper incisors: orthodont (0); inclined (1).
76. Enamel of upper and lower incisors: uncoloured (0); with colour (1).
77. Constriction of the apex at each lobe of the m1-m2: absent (0); present (1).
78. Transverse dentine crest on the occlusal surface, located at the middle of each molar lobe: absent (0); present (1).
79. Replacement of deciduous premolar: not replaced (0); with replacement (1).
80. Type of replacement: postnatal replacement (0); prenatal replacement (1).
81. Development of lobes in p4: incipient (0); well-developed (1).
82. \*Anterior projection on the prI of p4: absent (0); incipient (1); developed (2); like an incipient lobe (3); pr.s.a. (4).
83. Orientation of the prI of p4 when it has two well-developed lobes but without anterior projection: transverse (0); oblique (1).
84. \*Anterior flexid on the anterior wall of p4: absent (0); ephemeral (1); persistent (it persists to adult stages but disappears before reaching senile ontogenetic stages) (2); very persistent (it persists to senile ontogenetic stages) (3).
85. Lingual flexid (Longitudinal furrow opposite to the hypoflexid or hpi) on p4: absent (0); present (1). (Modified from Cerdeño et al., 2019 and Madozzo-Jaén, 2019).
86. Type of lingual flexid on p4: longitudinal furrow opposite to hypoflexid (0); hpi (=h1i) (1). (Modified from Cerdeño et al., 2019 and Madozzo-Jaén, 2019).
87. \*Depth of hpi on the occlusal surface of p4: shallow (0); up to 25% (1); up to 50% (2); up to 75% (3); more than 75% (3).
88. h2i (hsip sensu Mones 1991) on p4: absent (0); present (1).

89. Location of h2i on p4: prI (0); prII (1).
90. Depth of h2i on the occlusal surface of p4: shallow (up to 45%) (0); deep (more than 45%) (1).
91. h3i (hsia) or hsi (sensu Pérez *et al.* 2017) on p4: absent (0); present (1).
92. Location of h3i (hsia) or hsi (sensu Pérez *et al.* 2017) on p4: central (0); anterior (1).
93. Depth of h3i (hsia sensu Mones 1991) or hsi (sensu Pérez *et al.* 2017) on the occlusal surface of p4: shallow (0); deep (1).
94. Depth of h2i respect to h3i on the occlusal surface of p4: h2i deeper than h3i (0); equally deep (1); h2i shallower than h3i (2).
95. Orientation of h2i and h3i in prI of p4: parallel (0); convergent (1).
96. h5i on prsa of p4 when three lobes: absent (0); present (1).
97. \*Depth of h5i in prsa of p4: shallow, up to 25% (0); deep, up to 50% (1); very deep, more than 50% (2).
98. Depth of hpi with respect to h5i on the occlusal surface of p4: hpi deeper than h5i (0); hpi equally deep h.5i. (1).
99. hsni on p4: absent (0); present (1).
100. c3 in prI of p4: absent (0); present (1).
101. \*Development of c3 on prI of p4 when the h2i is located in prI: short (0); intermediate (1); long (2).
102. h3e on p4 (=hse or h2e sensu Mones 1991): absent (0); present (1).
103. Orientation of h3e (=hse or h2e sensu Mones 1991) on p4: transverse (0); oblique (1).
104. Depth of h3e (=hse or h2e sensu Mones, 1991) with respect to hfe on p4: h3e equally deep (0); h3e deeper than hfe (1); hfe deeper than h3e (2).
105. hse (= hse of m1, m2, and m3 sensu Mones) on p4 with three lobes: absent (0); present (1).
106. Developments of lobes in M1/m1–M2/m2: incipient lobes (0); developed lobes (1).
107. Symmetry of the lobes in each M1/m1–M2/m2, when the molars have furrow opposite to the hypoflexid: anterior and posterior lobes are asymmetrical (0); anterior and posterior lobes are symmetrical (1).
108. Shape of the anterior lobe of m1–m2: triangular (0); heart-shaped (1); lanceolate (leaf-shaped) (2); laminar, being less anteroposteriorly compressed than the anteroposterior diameter of the hypoflexid (3); strongly laminar, being equally or more anteroposteriorly compressed than the hypoflexid (4). (Modified by Candela and Bonini, 2017).
109. Shape of the posterior lobe of m1–m2: triangular (0); heart-shaped (1); complex heart-shaped (2).
110. hsi on m1–m2: absent (0); present (1).

111. \*Depth of hsi on m1–m2: shallow (0); less than 50% (1); approximately half of the prisms (50%) (2); more than 50% of the prism but not splitting (3).
112. hti in m1–m2: absent (0); present (1).
113. \*Depth of hti on m1: up to 50% of the prism (0); crossing the prism but not splitting (1); crossing and dividing the prism (2).
114. \*Depth of hti in m2: up to 50% of the prism (0); crossing the prism but not splitting (1); crossing and dividing the prism (2).
115. Depth of hsi respect to hti in m1: equally deep (0); hsi shallower than hti (1).
116. Lingual flexid (Longitudinal furrow opposite to the hypoflexid or hpi) on m1-m2: absent (0); present (1). (Modified from Cerdeño et al., 2019 and Madozzo-Jaén, 2019).
117. Type of lingual flexid on m1-m2: longitudinal furrow opposite to hypoflexid (0); hpi in m1-m2 (1). (Modified from Cerdeño et al., 2019 and Madozzo-Jaén, 2019).
118. Depth of hsi respect to hpi m1: equally deep (0); hsi shallower than hpi (1).
119. \*Depth of hpi in m1–m2: shallow (0); up to 25% (1); up to 50% (2); reaching the labial end (3); dividing the prism (4).
120. hse (sensu Mones 1991) on m1–m2: absent (0); present (1).
121. Depth of hse (sensu Mones 1991) on m1–m2: shallow (up to 39% of the width of the tooth) (0); deep (40% or more of the width of the tooth) (1).
122. \*Transverse extension of the hypoflexus/id (HFI, and hfe) in M1/m1-M2/m2 of adult stage: transversely shorter than half of the width of the crown (0); extending from the margin up to the transverse midpoint of the crown (1); extending beyond the transverse midpoint of the crown (2); crossing completely the tooth (3).
123. Hypoflexus/id (HFI and hfe), of M1/m1-M2/m2, forms a fossete/id with the ontogeny: yes (0); no (1).
124. Shape of the hypoflexus/id in occlusal view of M1/m1-M2/m2: very narrow and short (0); V-shaped (1); narrow and very long (2); funnel shaped (3); canal shaped (4); V-shaped with blunt end (5).
125. \*Antero-posterior length of p4–m1 with respect to m2–m3 (Wood and Patterson 1959): p4–m1 shorter than m2–m3 (0); p4–m1 approximately equal to m2–m3 (1); p4–m1 longer than m2–m3 (2).
126. Relative size of lower molars (antero-posterior length):  $m1 < m2 > m3$  (0);  $m1 < m2 < m3$  (1);  $m1 = m2 < m3$  (2);  $m1 = m2 = m3$  (3).
127. m3, when p4 has three lobes: simple (only hpi and hsi) (0); complex (hpi, hsi, hti and accessory flexids) (1).
128. hsi on m3: absent (0); present (1).
129. \*Depth of hsi in complex m3: shallow (0); deep (1); very deep (2).



130. Shape of prl in complex m3: laminar (narrow lobe) (0); curved lobe (posteriorly concave) (1); inverted U (lobe divided by the hsi) (2).
131. Transversal extension of hti and hsi on complex m3: not cross the occlusal surface (0); cross the occlusal surface (1).
132. Depth of hti with respect to hsi in complex m3 when they do not cross the occlusal surface: hsi deeper than hpi (0); hti and hsi equally deep (1).
133. \*Depth of hse (sensu Mones) on complex m3: very shallow notch (0); shallow (between 20%–70%) (1); deep (more than 75%) (2).
134. Orientation of left and right molar series: parallel to each other (0); anteriorly convergent (1).
135. Number of lobes in P4: one (0); two (1).
136. Shape of the anterior lobe of M1–M2: heart-shaped (0); laminar (1); lanceolate (leaf-shaped) (2).
137. Shape of the posterior lobe of M1–M2: triangular (0); heart-shaped (1).
138. Labial projection of the anterior lobe of M1–M2: absent (0); present (1).
139. Shape of the labial projection of the anterior lobe of M1–M2: tip shaped (0); rounded shaped (1).
140. HPE in M1–M2: absent (0); present (1).
141. Labial flexus (Longitudinal furrow opposite to the hypoflexus or HSE) on M1-M2: absent (0); present (1). (Modified from Cerdeño et al., 2019 and Madozzo-Jaén, 2019).
142. Type of labial flexus on M1-M2: longitudinal furrow opposite to the hypoflexus (0); HSE in M1-M2 (1). (Modified from Cerdeño et al., 2019 and Madozzo-Jaén, 2019).
143. Depth of the HPE respect to HSE: equally deep (0); HPE deeper than HSE (1); HSE deeper than HPE (2).
144. Relative size of the upper molars:  $P4 < M1 < M2$  (0);  $P4 > M1 < M2$  (1);  $P4 > M1 = M2$  (2);  $P4 > M1 > M2$  (3).
145. \*Number of lobes in M3: one (0); two (1); three (2); four (3); five–six (4); seven–ten (5); more than 10 (6).
146. Shape of posterior lobes in M3 when it has three or more lobes, in which the first lobe is heart-shaped: heart-shaped (0); lanceolate-shaped (1); laminar (2).
147. Pattern of the shape of lobes in M3 when it has three or more lobes: more than the first lobe are heart-shaped or lanceolate-shape (0); only the first lobe is heart-shaped or lanceolate-shaped and the others are laminar (1).
148. Posterior projection of the posterior lobe in M3, when the pattern is not laminar: absent (0); present (1).

149. \*Development of the posterior projection of the posterior lobe in M3 with two lobes: incipient projection (0); antero-posteriorly short (1); antero-posteriorly long (2); incipient lobe shaped (3).
150. \*Development of the posterior projection of the posterior lobe in M3 with three or more lobes, when the pattern is not laminar: incipient (0); like a small lobe (1).
151. External fissures in laminar prisms of M3: ephemeral or absent (0); present (1).
152. \* External fissures in first five laminar prisms in M3 with more than 10 laminar prisms: or absent or ephemeral (0); shallow (1); deep (2).

**Tegumentary characters**

153. Rhinarium (Campo et al. 2020): well defined (0); poorly defined (1).
154. Presence of hairs in the rhinarium (Campo et al. 2020): absent (0); present (1).
155. Hair distribution in the rhinarium (Campo et al. 2020): with bare area around nostrils (0); covering the entire surface (1).
156. Mystacial vibrissae (Campo et al. 2020): short and sparse (0); large and abundant (1).
157. Superciliary vibrissae (Campo et al. 2020): short (0); large (1).
158. Male genitalia (Campo et al. 2020): with two spikes at the base of the glandular sac (0); with no spikes at the base of the (1).
159. Genital and urinary orifices of the female (Campo et al. 2020): single small genitourinary orifice (0); genital and urinary orifices visible as separate (1).
160. Olfactory bulbs (Campo et al. 2020): small (0); large (1).

**Postcranial characters**

161. Manual digits (Campo et al. 2020): DIII subequal to DIV (0); DIII slightly larger than DIV (1); DIII digit larger than the DIV (2); DIII much larger than the DIV (3)
162. Length ulna bone with respect to length of skull: ulna shorter or equally length than skull (0); ulna longer than skull (1).
163. Length of shin bone with respect to length of skull: shin bone shorter than skull (0); shinbone longer than skull (1).
164. Length of radius with respect to length of humerus: radius shorter than humerus (0); radius longer than humerus (1).

**GenBank accession numbers.**

Family	Species	TTH	GHR	Cytochrome b	12S
Caviidae	<i>Cavia aperea</i>	AF433883.1	AF433930.1	GU136759.1	AF433908.1
	<i>Dolichotis patagonum</i>	AF433893.1	AF433939.1	AY382787.1	AF433917.1

	<i>Dolichotis salinicola</i>	AF433895.1	AF433941.1	GU136723.1	AF433919.1
	<i>Galea musteloides</i>	AF433885.1	AF433932.1	GU067527.1	AF433910.1
	<i>Galea spixii</i>	AF433888.1	AF433935.1	GU067492.1	AF433913.1
	<i>Hydrochoerus hydrochaeris</i>	AF433902.1	AF433948.1	GU136721.	U12454.1
	<i>Kerodon rupestris</i>	AF433891.1	AF433938.1	GU136722.1	AF433916.1
	<i>Microcavia australis</i>	AF433889.1	AF433937.1	AF491750.1	AF433915.1
Cuniculidae	<i>Cuniculus paca</i>	AF433880.1	AF433928.1	AY206570.1	AF520693.1
Dasyproctidae	<i>Dasyprocta</i>	AF433897.1	AF433942.1	AF437783.1	AF433921.1
Echimyidae	<i>Proechimys</i>	FJ865463.1	AF332039.1	U35414.1	U12447.1

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