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# **The tooth-bearing skeletal elements of the Italian urodeles, a comparative tool for osteological identification**

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1 **The tooth-bearing skeletal elements of the Italian urodeles, a comparative tool**  
2 **for osteological identification**

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11

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14

15 ***Running title:*** Tooth-bearing elements of Italian urodeles

16

17 **Abstract.** Urodele osteology is characterised by simplified skulls, loss of several bones and a specific  
18 sequence of cranial and limb ossification. The relatively few studies devoted to the comparative  
19 analysis of isolated urodele bones are mostly focused on the vertebrae and occipital complexes, and  
20 to a lesser extent humeri. The tooth-bearing skeletal elements (premaxillae, maxillae, dentaries, and  
21 vomers) are strongly neglected in this respect, despite being robust and as such sometimes found as  
22 fossils. Herein, we provide for the first time a comparative study of dentigerous bones, focusing on  
23 the Italian urodeles. Thirteen of the 19 species present in Italy, representing all genera except one,  
24 were analysed, for a total of 70 dry-prepared skeletons. The morphology of dentigerous skeletal  
25 elements of Italian urodeles is described and pictured, providing diagnostic characters and

26 dichotomous keys for the identification at the genus level in most cases, and species level in some.  
27 The diagnostic morphological characters were included in a phylogenetic analysis, the results of  
28 which demonstrate that the tooth-bearing elements can have a phylogenetic value useful for assessing  
29 the relationships of living taxa.

30

31 **Keywords.** Osteology, urodeles, phylogeny, dentigerous bones.

32

33

## INTRODUCTION

34 The Italian geographic province (Lanza & Corti, 1996) shows the highest amount of urodele  
35 endemism in Europe (Macaluso et al. 2021a, b, 2023a), including three endemic genera  
36 (*Salamandrina*, *Speleomantes*, and *Euproctus*; Lanza et al., 2007). How and when these taxa reached  
37 the Italian Peninsula is not yet fully understood as the Italian fossil record of urodeles is poor, mostly  
38 composed of isolated remains identified at best to the genus level, in a chronologic range spanning  
39 from the Miocene to the Holocene (among others, Abbazzi et al., 2004; Colombero et al., 2017;  
40 Delfino, 2004; Delfino et al., 2011; Delfino & Bailon, 2000; D’Orazi Porchetti et al., 2012; Macaluso  
41 et al., 2021a; Venczel & Sanchiz, 2006; Villa et al., 2018, 2020, 2021). Besides the rarity of fossils,  
42 our knowledge of the fossil record of urodeles is hindered by the limited studies on the osteology of  
43 the extant species. In fact, even if some studies focus on extensive and comprehensive descriptions  
44 of one taxon or a few taxa, few studies were devoted to the comparative analysis of isolated bones  
45 that represent nearly the entire Italian fossil record. At a European scale, the only inclusive and  
46 comparative studies are focused on vertebrae, otic-occipital complexes, and humeri (Ratnikov &  
47 Litvinchuk, 2007, 2009; Ratnikov, 2015; Macaluso et al., 2023b), which are the most commonly  
48 found elements in the fossil record thanks to their general robustness (Monti, 2021; Macaluso et al.,  
49 2022). Among the skull elements (the second most common skeletal district in the fossil record  
50 composed of isolated remains; Monti, 2021; Macaluso et al., 2022), tooth-bearing skeletal elements  
51 (premaxillae, maxillae, dentaries, and vomers) are easily found because of their peculiar morphology

52 and relative thickness. Despite being easily recognised as belonging to Urodela or Amphibia due to  
53 the pedicellate teeth (Schoch, 2014), a generic or specific attribution is rarely reached because of a  
54 lack of comparative studies on the dentigerous elements. The aim of the current work is to provide  
55 taxonomically significant diagnostic characters at least at the genus level, and, when possible, at the  
56 species level, for Italian urodeles based on isolated dentigerous bones, as well as a dichotomous key  
57 for identification. Moreover, to provide a scaffold for the inclusion in phylogenies of extinct taxa, the  
58 most robust diagnostic morphological characters are included in a character matrix to test whether or  
59 not the tooth-bearing elements carry phylogenetic value useful for assessing the relationships of living  
60 (and therefore also extinct) taxa.

61

62

#### MATERIAL AND METHODS

63 The morphology of dentigerous skeletal elements of Italian urodeles is described based on  
64 disarticulated dry-prepared skeletons, housed in the Massimo Delfino Herpetological collection  
65 (MDHC) of the Museo di Geologia e Paleontologia dell'Università di Torino (MGPTU), at the  
66 Department of Earth Sciences of the University of Turin, and in the Museo Regionale di Scienze  
67 Naturali di Torino (MRSN). Thirteen of the 19 species present in Italy are considered, including two  
68 families, Plethodontidae and Salamandridae, and seven genera, for a total of 70 specimens (Table S1)  
69 and approximately 560 bones. All Italian genera are represented except *Proteus*, which is not included  
70 in this study due to its peculiar and derived morphology (noteworthy is the absence of maxillae; Fabre  
71 et al., 2020) and will be the subject of future studies. All the missing species belong to the genus  
72 *Speleomantes*: this study includes *Speleomantes ambrosii*, *Speleomantes italicus*, and *Speleomantes*  
73 *strinatii*, whereas the species *Speleomantes supramontis*, *Speleomantes sarrabusensis*, *Speleomantes*  
74 *flavus*, *Speleomantes genei*, and *Speleomantes imperialis* are missing. For some taxa (*S. ambrosii*, *S.*  
75 *italicus*), only one specimen has been studied, whereas for others (*Salamandra salamandra*, *Triturus*  
76 *carnifex*) as many as 11 specimens were examined. Moreover, for *Salamandra atra*, only one broken  
77 left vomer was available and *S. atra* MDHC 394 is represented by two specimens (MDHC394a and

78 b). For *S. italicus* MDHC 301, only the left maxilla and the dentaries are present. *Euproctus*  
79 *platycephalus* MDHC 405 does not preserve any dentigerous bone except for the dentaries. As such,  
80 it is important to underline that the characters concerning poorly represented species should be taken  
81 with caution due to the limited number of available specimens. Bones were photographed with a  
82 Leica M205 microscope equipped with the Leica application suite v3.3.0 or v4.10 at the Department  
83 of Earth Sciences of the University of Turin. Terminology follows Vater (2003), Buckley et al.  
84 (2010), and Villa et al. (2014).

85

#### 86 *Comparative and phylogenetic analysis*

87 Dichotomous keys for identification and diagnostic characters were obtained comparing the  
88 descriptions and the observations made on the different taxa and are reported in the discussion section  
89 below. We performed statistical counts on the teeth number using Excel v2307.

90 A character matrix, including 13 species-level operational taxonomic units and 33 newly created  
91 osteological characters (supplementary file F1), was built with Mesquite v3.61 (Maddison and  
92 Maddison, 2019). All characters are related to the dentigerous bones (see Table S2 for the list of the  
93 characters). The hynobiid *Pseudohynobius flavomaculatus* was scored as outgroup, owing to its  
94 phylogenetic distance from the other operational taxonomic units (Duellman & Trueb, 1994; Kohono  
95 et al., 1991; Pyron & Wiens, 2011) and basing the scoring on the descriptions and pictures by Jia et  
96 al. (2021).

97 The phylogenetic analysis was run using TNT v1.6 (Goloboff & Morales, 2023) using the New  
98 Technology search with all algorithms selected, the consensus stabilised five times with a factor of  
99 75, and 1000 trees in memory, followed by a second round of tree bisection and reconnection.

100

101

## RESULTS

### 102 *Terminology and general morphology*

103 The anatomical structures cited in the text are illustrated in Fig. 1.

104 Premaxilla. Premaxillae are paired bones placed at the anterior end of the skull; they articulate  
105 medially with each other, laterally with the maxillae and posteriorly with the vomers. They can be  
106 separated or fused together, and they are formed by three main parts: alary process, pars dentalis, and  
107 pars palatina. The alary process is thin, dorsally elongated and curved in posterodorsal direction; it  
108 contacts the anterior end of the frontal, and its posterior half is partially overlapped by the nasal. The  
109 pars dentalis bears a variable number of pedicellate teeth, which can be seen in anterior and lateral  
110 views, and it is slightly curved, usually thicker than the alary process; the dorsal margin can be straight  
111 or irregular. The pars dentalis articulates with the maxilla through the margo maxillaris. The pars  
112 palatina is always visible in posterior view. The margo vomeropalatinum can be straight or may show  
113 some irregularities.

114 Maxilla. Maxillae are paired bones, which articulate anteriorly with the premaxillae, dorsally with  
115 the prefrontals and nasals and medially with the vomers; their posterior end does not contact the  
116 pterygoid and extends only slightly beyond the posterior margin of the eye, without reaching the  
117 quadrate. Maxillae are formed by three main parts: pars facialis, pars dentalis, and pars palatina. The  
118 pars facialis develops in dorsal direction, it has a trapezoidal shape with irregular margins, and it can  
119 be smooth or sculptured. It articulates with the prefrontal and the nasal through respectively the margo  
120 praefrontalis and the margo nasalis and with the premaxillae through the processus maxillaris  
121 anterior. The margo anterioris and the margo orbitalis can be straight or irregular. The pars dentalis  
122 is narrow, regular and elongated and bears a variable number of pedicellate teeth that can be visible  
123 both in lateral and medial views; the pars dentalis can be straight or curved posterodorsally. The  
124 sulcus dentalis is visible on the medial surface of the pars dentalis, dorsally to the teeth. The pars  
125 palatina allows the whole maxilla to articulate with the corresponding premaxilla and can have  
126 variable shapes.

127 Dentary. Dentaries are elongated, paired and curved bones. They are robust and they are the primary  
128 bones forming the mandible. They touch each other anteromedially at the symphysis and their  
129 posterior portion articulates medially with prearticulars and articulars. The processus articularis is

130 laminar. Posteriorly the bone is flat and smooth, with a pointy or rounded shape. The dorsal and  
131 ventral margins of the bone tend to fold up and they can be fused to a varying degree; due to the  
132 folding, the two margins are thicker than the bone between them. The two margins cover the canalis  
133 primordialialis, which runs along the whole medial surface of the dentary. The space between the two  
134 margins is called the incisura dentalis, that is straight and regular and narrows in the anterior part due  
135 to the margins approaching. The latter come in contact in some species. The crista dentalis bears a  
136 variable number of pedicellate teeth, extending up to the processus coronoideus, a little triangular or  
137 trapezoidal expansion that sometimes is absent and likely changes significantly through ontogeny.

138 Vomer. Vomers are paired elements that articulate anterolaterally with the premaxillae through the  
139 margo intermaxillaris and with the maxillae through the margo maxillaris. Dorsally, the vomers  
140 articulate with the parasphenoid and orbitosphenoids through respectively the margo  
141 parasphenoideum and the margo orbitosphenoideum. The two vomers do not touch each other. This  
142 bone is made by two parts: the body of the vomer and the dentigerous ridge. The body of the vomer  
143 has a triangular or a claw hammer shape and it develops in a posterior direction; it is smooth on both  
144 the dorsal and ventral surfaces, and it keeps the same thickness throughout. The body of the vomer  
145 shows a concavity on the margo choanalis, bounded by the processus vomeropalatinus major and the  
146 processus vomeropalatinus minor, which can be variably pronounced or even absent. Only in  
147 *Speleomantes*, the concavity is bounded by the processus vomeropalatinus major and the dentigerous  
148 ridge. The dentigerous ridge is elongated and bears a variable number of pedicellate teeth that are  
149 regularly visible in lateral view. Dorsally to the teeth there is a very shallow sulcus dentalis. In *T.*  
150 *carnifex* and *S. salamandra*, there can be an aberrant condition with some supernumerary teeth  
151 developing outside the normal dental line.

152

153 *Descriptions*

154 In this section, the morphology of premaxillae (Figs. 2, 3), maxillae (Figs. 4, 5), dentaries (Figs. 6,  
155 7), and vomers (Fig. 8) are described for each taxon. The counts of the tooth positions are summarized  
156 in Table S3 (and discussed below in the section “Variation in the number of tooth positions”).

157

158 Plethodontidae

159 *Speleomantes*

160 The species of the genus *Speleomantes* are grouped into a single description, emphasizing the  
161 differences between species.

162 Premaxilla (Fig. 2A-L). The premaxillae of the only studied specimen of *S. italicus* are missing. In  
163 *Speleomantes*, the two premaxillae are not fused together. Only in *S. strinatii* MDHC 225, the two  
164 premaxillae are fused together: they are connected by a thin bridge well visible in anterior and  
165 posterior views on the ventral third of the medial margin of the alary process. This bridge is pierced  
166 by one foramen. The whole premaxilla of *Speleomantes* is three times higher than long. In lateral  
167 view, it shows an expansion that extends along its dorsal half. The dorsal half of the alary process  
168 ends with a rounded tip. The pars dentalis is of the same thickness as the alary process and it is  
169 straight. The margo maxillaris is medially rounded. In posterior view, the pars palatina is developed  
170 in posterior direction, but it is not visible in anterior view, as it is covered by the dorsal half of the  
171 pars dentalis. It is subtriangular in shape, enlarging posterolaterally.

172 Maxilla (Fig. 4A-L). In *S. ambrosii*, the pars facialis extends along the middle third of the crista  
173 dentalis. In *S. italicus* and *S. strinatii*, the pars facialis extends respectively along the second fourth  
174 and the second and third fifths (MDHC 225) or the middle third (MDHC 486 and MDHC 521) of the  
175 crista dentalis. It has a smooth surface, both in lateral and medial views. In lateral view, it shows a  
176 shallow concavity on the margo orbitalis and another one on the margo anterioris; these cavities are  
177 absent in *S. italicus*. The margins are rather straight in *S. ambrosii* and *S. italicus*, and irregular in *S.*  
178 *strinatii*. The right pars facialis of MDHC 225 shows one foramen. The teeth run for the whole length  
179 of the pars dentalis, including the processus maxillaris anterior. As such, the pars facialis does not

180 reach the anterior end of the tooth row. The pars palatina runs along the whole dorsomedial margin  
181 of the pars dentalis. This pars is very small, with the same width for almost its entire length; it ends  
182 anteriorly in a flat and abrupt processus maxillaris anterior, with regular margins.  
183 Dentary (Fig. 6A-L). The margins fold up covering the anterior third of the canalis primordialis,  
184 which runs across the whole medial surface of the dentary, so that in medial view the incisura dentalis  
185 opens only along its posterior two thirds. In *S. strinatii*, only the ventral margin of the dentary folds  
186 up, thickening and covering a small part of the canalis primordialis. In medial view, the processus  
187 coronoideus has a parallelogram-like shape, with smooth edges. In *S. italicus*, the processus  
188 coronoideus is almost absent. The symphysis shows an anterodorsal bulge in medial view. In ventral  
189 view, in *S. strinatii*, the ventral margin is thicker than the dorsal one.  
190 Vomer (Fig. 8A-F). The vomers of *S. italicus* are missing. In ventral view, the body of the vomer has  
191 a triangular shape, with a laterally directed tip. In dorsal and medial views, the margo choanalis shows  
192 a concavity bounded by the processus vomeropalatinus major and the dentigerous ridge. The  
193 dentigerous ridge is mediolaterally directed, slightly posteriorly curved, forming with the margo  
194 intervomeropalatinum an acute angle. In lateral view, the dentigerous ridge is curved. The margo  
195 intervomeropalatinum and the margo maxillaris are regular and rather straight.

196

197 Salamandridae

198 Salamandrinae

199 *Salamandra lanzai*

200 Premaxilla (Fig. 2I-L). The two premaxillae are not fused together. The premaxilla is as long as or  
201 slightly shorter than high. In anterior view, the alary process ends abruptly. Still in the same view,  
202 the pars dentalis is thick, rectangular and curved posterolaterally, with either one or two foramina on  
203 its dorsal half. In dorsal view, the ventral half of the premaxilla is thickened at the articulation with  
204 the opposite premaxilla. In anterior view, the margo maxillaris is vertical. The margo  
205 vomeropalatinum is generally straight in dorsal view, but it can show some irregularity. The dorsal

206 margin of the pars dentalis expands in posterior direction and, together with the expansion of the alary  
207 process, it forms a cavity, open on the anterior side. Dorsally to this cavity, there is another smaller  
208 one (missing on the right premaxilla of MDHC 362). The pars palatina is extremely small and cannot  
209 be seen in anterior view. In posterior view, the pars palatina keeps the same width for all its length,  
210 except for a widening at midlength.

211 Maxilla (Fig. 4M-P). In lateral view, the pars facialis bears one to three foramina and has a variable  
212 thickness. The pars facialis extends along the anterior half of the pars dentalis. In lateral and medial  
213 views, the margo anterioris is particularly irregular, with sharp edges, whereas the margo orbitalis is  
214 more regular and straight. Only the posterior fourth of the length of the pars dentalis is toothless. The  
215 pars palatina runs along the whole dorsomedial margin of the pars dentalis; it keeps the same width  
216 for almost its entire length, forming a triangular and sharp processus maxillaris anterior, with irregular  
217 margins. The pars facialis does not significantly extend on the processus maxillaris anterior, but it  
218 ends together with the tooth row anteriorly. In ventral view, the pars palatina of the left maxilla of  
219 MDHC 361 expands medially with a V-shaped tip, whereas the pars palatina of MDHC 363, MDHC  
220 465, and MDHC 450 forms a medial triangular expansion with irregular margins by the posterior  
221 margin of the pars facialis. This triangular expansion is interrupted by one or two foramina, well  
222 visible in ventral view.

223 Dentary (Fig. 6M-P). The symphysis is semicircular in medial view. The dorsal and ventral margins  
224 are not fused together, so that in medial view the incisura dentalis is fully open. Conversely, in MDHC  
225 465, the two margins are fused together and the incisura dentalis is not visible. In medial view, the  
226 processus coronoideus is particularly small and it has a parallelogram-like shape, with smooth edges  
227 (in MDHC 362, it is almost not visible).

228 Vomer (Fig. 8G-I). In dorsal view, the body of the vomer has a triangular shape, with a tip facing  
229 anteriorly. In dorsal view, the margo maxillaris forms a continuous convex anterolateral margin. The  
230 body of the vomer develops in posterodorsal direction. The processus vomeropalatinus minor is  
231 poorly developed. The dentigerous ridge forms an angle of ca. 130° with the margo

232 intervomeropalatinum in ventral and dorsal views. In ventral view, the dentigerous ridge is elongated  
233 and has a slightly sigmoid shape, with an anteromedially directed anterior end and a posterolaterally  
234 directed posterior end. The width of the dentigerous ridge is the same in the anterior two thirds of its  
235 length, whereas the posterior third can become narrower. Almost all vomers are broken.

236

237 *Salamandra atra*

238 Premaxilla (Fig. 2M-P). The two premaxillae are not fused together. The premaxilla is as long as or  
239 slightly shorter than high. In anterior view, the alary process ends abruptly. A medial cavity is present  
240 on the medial margin of this process. Still in anterior view, the pars dentalis is as thick as the alary  
241 process, rectangular and curved posterolaterally. The left premaxilla of MDHC 394a bears one  
242 foramen. In dorsal view, the ventral half of the premaxilla is thickened at the articulation with the  
243 opposite premaxilla. In anterior view, the margo maxillaris is vertical. The margo vomeropalatinum  
244 is straight in dorsal view. The dorsal margin of the pars dentalis expands in posterior direction and,  
245 together with the expansion of the alary process, it forms a cavity, open on the anterior side. The pars  
246 palatina is poorly developed but can be seen in anterior view too. In posterior view, the pars palatina  
247 develops in dorsal direction and keeps the same width for all its length, except for a widening at  
248 midlength.

249 Maxilla (Fig. 4Q-T). In lateral view, the pars facialis bears one or two foramina and has a variable  
250 thickness. The pars facialis extends along the anterior half of the pars dentalis. In MDHC 394a, in  
251 lateral and medial views, the margo anterioris is particularly irregular, with sharp edges, whereas the  
252 margo orbitalis is more regular and straight. Conversely, in MDHC 394b, both margins are straight.  
253 Only the posterior fifth of the length of the pars dentalis is toothless. The pars palatina runs along the  
254 whole dorsomedial margin of the pars dentalis; it narrows at the anterior end, forming a triangular  
255 and sharp processus maxillaris anterior with irregular margins. The pars facialis does not significantly  
256 extend on the processus maxillaris anterior, but it ends together with the tooth row anteriorly. In  
257 ventral view, the pars palatina forms a medial triangular expansion with irregular margins by the

258 posterior margin of the pars facialis. This triangular expansion is pierced by two foramina, well visible  
259 in ventral view. In the left maxilla of MDHC 394a, the medial margin of the pars palatina is broken  
260 at the level where the foramina should be located, resulting in the presence of a medially open  
261 concavity in place of the latter. The right maxilla of MDHC 394b is broken, thus, the presence of  
262 foramina or cavities cannot be evaluated.

263 Dentary (Fig. 6Q-T). The symphysis is semicircular in medial view. The dorsal and ventral margins  
264 are fused together in the anterior half of the dentary, so that in medial view the incisura dentalis opens  
265 only along its posterior half. Conversely, in MDHC 394b, the two margins do not completely fold up;  
266 they rise in the anterior half, giving to the bone a concave shape. In this same specimen, the canalis  
267 primordialialis is, thus, fully visible. In the posterior half, the two margins are almost flat, and the bone  
268 widens. On the left dentary of MDHC 394a, there are no tooth positions on the anterior fourth of the  
269 bone. In medial view, the processus coronoideus is particularly small and it has a parallelogram-like  
270 shape, with irregular edges. Even if MDHC 394b shows unfolded margins, the latter are still thicker  
271 than the rest of the bone in this specimen as well.

272 Vomer (Fig. 8J). Vomers of MDHC 394a and the right vomer of MDHC 394b are missing, so the  
273 description is based on the broken left vomer of MDHC 394b. In dorsal view, the body of the vomer  
274 has a triangular shape, with a tip facing anteriorly. In the same view, the margo maxillaris forms a  
275 continuous convex anterolateral margin. The body of the vomer develops in posterodorsal direction.  
276 The processus vomeropalatinus minor is poorly developed. The dentigerous ridge forms an angle of  
277 ca. 130° with the margo intervomeropalatinum in ventral and dorsal views. In ventral view, the  
278 dentigerous ridge is elongated and has a slightly sigmoid shape, with an anteromedially directed  
279 anterior end and a posterolaterally directed posterior end. The width of the dentigerous ridge is the  
280 same in the anterior two thirds of its length, whereas the posterior third can become narrower. In  
281 ventral view, the dentigerous ridge bears on the anterior third some teeth that are not visible in lateral  
282 and dorsal views. This happens because the lateral margin of the body of the vomer expands ventrally  
283 to cover the dentigerous ridge.

284

285 *Salamandra salamandra*

286 Premaxilla (Fig. 2Q-T). The two premaxillae are not fused together. The premaxilla is as long as or  
287 slightly shorter than high. In anterior view, the alary process ends with a dorsal rounded or sharp tip.  
288 In posterior view, on the dorsal half of the pars dentalis, the medial margin can form two or three  
289 triangular expansions. In dorsal view, on the dorsal half of the pars dentalis, foramina can be either  
290 present or absent, varying in number from zero to three. In lateral view, in both premaxillae of MDHC  
291 23, in the left premaxilla of MDHC 124, and in the right premaxilla of MDHC 227, there is a cavity  
292 on the medial margin of the alary process. In anterior view, the pars dentalis is of the same thickness  
293 of the alary process, rectangular and, in dorsal view, it curves posterolaterally. In dorsal view, the  
294 ventral half of the premaxilla is thickened at the articulation with the opposite premaxilla. In anterior  
295 view, the margo maxillaris is vertical. The margo vomeropalatinum is straight in dorsal view. In the  
296 same view, the dorsal margin of the pars dentalis expands in posterior direction and, together with  
297 the expansion of the alary process, it forms a cavity, open on the anterior side. Posterior to this cavity,  
298 there is another smaller cavity (absent in MDHC 23, MDHC 227, MDHC 234, and MDHC 396). The  
299 pars palatina is poorly developed but can be seen in anterior view too. In posterior view, the pars  
300 palatina develops in dorsal direction and keeps the same width for all its length; only at midlength, it  
301 widens and forms a triangular expansion.

302 Maxilla (Fig. 4U-Y). In lateral view, the pars facialis bears two to six foramina and has a variable  
303 thickness. The pars facialis extends along the anterior third of the pars dentalis. In lateral and medial  
304 views, the margo anterioris is particularly irregular with sharp edges. The margo orbitalis is irregular  
305 too. In MDHC 124 and MDHC 387, the margo anterioris is vertical, forming a right angle in the  
306 ventral end, whereas in MDHC 234 and MDHC 235, it is semicircular. The pars dentalis can be  
307 straight or bend posteroventrally in the posterior half (the anterior half is always anterodorsally  
308 directed). Only the posterior fourth of the length of the pars dentalis is toothless. The pars palatina  
309 runs along the whole dorsomedial margin of the pars dentalis; it keeps the same width for almost its

310 entire length, forming a triangular and sharp processus maxillaris anterior, with regular margins. The  
311 pars facialis does not significantly extend on the processus maxillaris anterior but it ends together  
312 with the tooth row anteriorly. In ventral view, the pars palatina forms a medial triangular expansion  
313 with irregular margins by the ventral half of the pars facialis. This triangular expansion is pierced by  
314 one to three foramina, well visible in ventral view. Between the pars palatina and the pars facialis,  
315 there are one to three cavities, well visible in dorsal view. In the left maxilla of MDHC 205 and  
316 MDHC 212, the cavities are not separated, resulting in a larger one. In dorsal view, both maxillae of  
317 MDHC 227 and the left one of MDHC 234 show one foramen, anteriorly to the cavities.

318 Dentary (Fig. 6U-X). The symphysis is semicircular in medial view. In dorsal view, the anterior third  
319 of the right dentary of MDHC 23 bends medially, forming an almost right angle. The anterior half of  
320 the dorsal and ventral margins are fused together, so that in medial view the incisura dentalis opens  
321 only along its posterior half. In MDHC 212 and the left dentary of MDHC 364, the margins are not  
322 fused in the second fourth of the dentary from the anterior end, so that the incisura dentalis opens in  
323 this part of the bone and closes again posteriorly. In MDHC 124, MDHC 234, MDHC 235, and  
324 MDHC 387, on the other hand, the margins fuse only in the anterior fourth of the dentary. In dorsal  
325 view, between the folding of the dorsal margin and the crista dentalis, there are two to four foramina.  
326 In medial view, by the processus coronoideus, the dorsal margin of the bone is completely flat. Still  
327 in the same view, the processus coronoideus is particularly small and it has a parallelogram-like  
328 shape, with smooth edges.

329 Vomer (Fig. 8K-M). In dorsal view, the body of the vomer has a triangular shape, with a tip facing  
330 anteriorly. In the same view, the margo maxillaris forms a continuous convex anterolateral margin.  
331 The body of the vomer develops in posterodorsal direction. In dorsal and ventral views, there are two  
332 concavities at the centre of the margo choanalis: the largest one is bounded by the processus  
333 vomeropalatinus major and the processus vomeropalatinus minor, which is small and pointy, whereas  
334 the smallest one is posteromedial to the processus vomeropalatinus minor. The left vomer of MDHC  
335 212 and both vomers of MDHC 386 show just one concavity. In ventral view, the dentigerous ridge

336 is elongated and has a slightly sigmoid shape, with an anteromedially directed anterior end and a  
337 posterolaterally directed posterior end. The width of the dentigerous ridge is the same in the anterior  
338 two thirds of its length, whereas the posterior third becomes narrower. The dentigerous ridge forms  
339 an angle of ca. 130° with the margo intervomeropalatinum in ventral and dorsal views. In lateral view,  
340 the dentigerous ridge is strongly curved. In ventral view, the dentigerous ridge bears on the anterior  
341 third some teeth that are not visible in lateral and dorsal view. This happens because the lateral margin  
342 of the body of the vomer expands ventrally to cover the dentigerous ridge. In ventral view, between  
343 the dentigerous ridge and the body of the vomer, there can be one to four cavities. The vomers of  
344 MDHC 386 do not show any cavity and the right vomer of MDHC 235 shows one foramen instead  
345 of the cavity. The teeth on the dentigerous ridge are not properly aligned in a row.

346

347 *Salamandrininae*

348 The species of the genus *Salamandrina* are grouped into a single description, emphasizing the  
349 differences between species.

350 *Salamandrina*

351 Premaxilla (Fig. 2U-AB). The two premaxillae are not fused together. The premaxilla is as long as or  
352 slightly shorter than high. In anterior view, the alary process shows a thickening on its medial margin,  
353 which extends for the two ventral thirds of the alary process and makes the whole process thick and  
354 sturdy. The expansion is visible also in lateral view, giving to the process a semicircular shape. In  
355 dorsal view, the ventral half of the premaxilla is thickened at the articulation with the opposite  
356 premaxilla. Between the ridge and the alary process there are one to four foramina. Only MDHC 495  
357 shows no ridge or foramina. In anterior view, on the alary process one can find two to six foramina,  
358 which concentrate on the thick expansion. MDHC 495 shows no foramina in the alary process. In  
359 anterior view, the pars dentalis is thick, rectangular and curved posterolaterally. In anterior view, the  
360 margo maxillaris is vertical. The margo vomeropalatinum is straight in dorsal view. In posterior view,  
361 the pars palatina develops in dorsal direction, medially enlarging. The posterior half of the alary

362 process is not visible in posterior view. In posterior view, the pars palatina of MDHC 407 is pierced  
363 by three foramina, whereas the left premaxilla of MDHC 342 bears one foramen. The pars palatina  
364 is well developed and it is visible in anterior view too. In lateral view, between the pars palatina and  
365 the pars dentalis, a foramen is visible at the dorsal margin of the pars dentalis. The cavities defined  
366 by the dorsal margin of the pars dentalis and the expansion of the alary process, which are present in  
367 the specimens of the genus *Salamandra*, are absent.

368 Maxilla (Fig. 4Z-AG). In lateral view, the pars facialis shows two to six foramina and has a variable  
369 thickness. In lateral view, the pars facialis shows one to four cavities, forming a shallow sculpturing  
370 composed only of depressions and with no crests (except for MDHC 228, that shows no cavity). The  
371 pars facialis extends along the anterior third of the pars dentalis. In medial view, the dorsal half of the  
372 pars facialis shows a triangular medial expansion. This expansion develops in dorsal direction in  
373 *Salamandrina perspicillata* and is not visible in lateral view, whereas it is posterodorsally directed  
374 and visible also in lateral view in *Salamandrina terdigitata*. The margo anterioris and the margo  
375 orbitalis are regular, except for the left maxillae of MDHC 228 and MDHC 300, which are the only  
376 maxillae with an irregular margo orbitalis. In medial view, the processus maxillaris posterior is thick  
377 and dorsoventrally expanded; it is also posterodorsally directed, giving a semicircular shape to the  
378 whole pars dentalis. In dorsal view, the pars dentalis shows one to three cavities; MDHC 492 and  
379 MDHC 495 do not show any cavity. In lateral view, the pars dentalis, along its length, shows one to  
380 three foramina; however, no foramina are present on the pars dentalis of the maxillae of MDHC 407,  
381 MDHC 492, and MDHC 494. Only the anterior fourth of the length of the pars dentalis is toothed.  
382 The pars palatina runs along the anterior third of the dorsomedial margin of the pars dentalis. In  
383 medial view, the pars palatina narrows at the anterior end, forming a triangular and sharp processus  
384 maxillaris anterior, with regular margins. The pars facialis extends more anteriorly than the tooth row,  
385 on the processus maxillaris anterior. In ventral view, the pars palatina has a semicircular shape with  
386 irregular margins. In dorsal view, between the pars palatina and the pars facialis, there are two

387 cavities. Exceptions to this are the right maxillae of MDHC 406, in which the two cavities are replaced  
388 by two foramina, and MDHC 494, showing only one cavity.

389 Dentary (Fig. 6Y-AF). The symphysis is semicircular in medial view. Posteriorly the bone is pointed.  
390 The dorsal and ventral margins are completely fused together, closing completely the incisura  
391 dentalis. In dorsal view, between the dorsal margin that folded up and the crista dentalis, the right  
392 dentary of MDHC 228 and both dentaries of MDHC 407 show one foramen. In medial view, by the  
393 processus coronoideus, the dorsal margin of the bone is completely flat. The processus coronoideus  
394 is almost absent in all specimens, but MDHC 300 displays a prominent and triangular process.

395 Vomer (Fig. 8N-S). In dorsal view, the margo maxillaris forms a continuous convex anterolateral  
396 margin, which can be provided with sharp edges. In dorsal view, the anteromedial tip of the body of  
397 the vomer forms an expansion followed by a deep concavity that interrupts the margo  
398 intervomeropalatinum, which is otherwise straight. This structure gives the vomer a characteristic  
399 shape that resembles a claw hammer. The body of the vomer develops in posterodorsal direction. The  
400 processus vomeropalatinus minor is short. In ventral view, the dentigerous ridge is elongated and  
401 curved, forming a lateral concavity and having an anterolaterally directed anterior end and a  
402 posterodorsally directed posterior end. The width of the dentigerous ridge is the same in the anterior  
403 two thirds of its length, whereas the posterior third becomes narrower. The dentigerous ridge forms  
404 an angle of ca. 180° with the margo intervomeropalatinum in ventral and dorsal views. In lateral view,  
405 the dentigerous ridge is straight (or slightly curved). In ventral view, the dentigerous ridge bears on  
406 the anterior fourth some teeth that are not visible in lateral and dorsal view. This happens because the  
407 lateral margin of the body of the vomer expands ventrally to cover the dentigerous ridge.

408

409 Pleurodelinae

410 *Euproctus platycephalus*

411 Premaxilla (Fig. 3E-H). The two premaxillae are fused together forming a single bone; they are  
412 connected through the whole medial margin of the pars dentalis and half of the alary process. The

413 dorsal halves of the alary processes remain close along all their length. In anterior view, the alary  
414 process bears one (MDHC 508) or seven (MDHC 507) foramina and it is weakly sculptured. The pars  
415 dentalis is of the same thickness as the alary process and it is curved; it bears three foramina on the  
416 ventral margin and another larger one where the left and right partes dentalis meet. The margo  
417 maxillaris is concave. In posterior view, the pars palatina is well developed posterodorsally, and it is  
418 visible also in anterior view. It keeps approximately the same width for its entire length and has  
419 regular margins.

420 Maxilla (Fig. 5E-H). The pars facialis extends along the anterior half of the crista dentalis and it has  
421 a smooth surface in medial view, whereas in lateral view the surface is sculptured, with irregular pits  
422 and ridges. In lateral view, the right maxilla of both MDHC 508 and MDHC 509 show three larger  
423 cavities, whereas the left maxilla of MDHC 509 shows two smaller cavities. MDHC 507 hosts five  
424 larger cavities, positioned in a straight line on the ventral margin. The left maxilla of MDHC 508  
425 bears two foramina. In medial view, the right maxilla of MDHC 508 shows three cavities on the  
426 anterior margin and a foramen between the pars dentalis and the pars facialis. Between the pars  
427 facialis and the pars dentalis, one (left maxilla of MDHC 507, MDHC 508, right maxilla of MDHC  
428 509) or two (right maxilla of MDHC 507, left maxilla of MDHC 509) foramina can be seen. In lateral  
429 view, on the pars dentalis of MDHC 508, three cavities can be seen. In posterior view, the pars facialis  
430 of the left maxilla of MDHC 508 has two cavities and one foramen on the anterior margin. In lateral  
431 view, on the margo anterioris of MDHC 508, two pointed expansions are visible. In medial view, the  
432 processus maxillaris posterior is covered by a ridge formed by the pars palatina. Less than the  
433 posterior sixth of the pars dentalis is toothless. The pars palatina runs along the whole dorsomedial  
434 margin of the pars dentalis, keeping the same width for the anterior half of the latter. It narrows at the  
435 anterior end without meeting the pars facialis, so the triangular and sharp processus maxillaris anterior  
436 is formed just by the pars facialis. The pars facialis extends more anteriorly than the anterior end of  
437 the tooth row.

438 Dentary (Fig. 7A-D). In medial view, the processus articularis is as thick as the rest of the bone.  
439 Posteriorly, the bone is pointed. The anterior half of the dorsal and ventral margins are fused together,  
440 so that in medial view the incisura dentalis opens only along the posterior half of the dentary. In  
441 MDHC 508, the two margins are fused for the anterior two thirds. In lateral view, three to seven  
442 foramina are visible. In medial view, the processus coronoideus has a triangular shape with smooth  
443 edges. The symphysis shows a dorsal bulge in the same view.

444 Vomer (Fig. 8W-Y). In dorsal view, the body of the vomer has a triangular shape, with a tip facing  
445 anteromedially. Still in the same view, the margo maxillaris forms a continuous convex anterolateral  
446 margin. The body of the vomer develops in posterodorsal direction, forming a pointy extension. The  
447 processus vomeropalatinus minor is poorly developed. On the margo intervomeropalatinum, there is  
448 a triangular expansion dorsally directed. In ventral and dorsal views, the dentigerous ridge is straight  
449 and elongated; it forms an angle of ca. 180° with the margo intervomeropalatinum. In lateral view,  
450 the dentigerous ridge is straight (or slightly curved). The margo orbitosphenoideum forms an  
451 expansion that runs for the two anterior thirds of the dentigerous ridge; in the last third, it ends  
452 suddenly. All the teeth are visible in lateral and dorsal views.

453

454 *Triturus carnifex*

455 Premaxilla (Fig. 3A-D). The two premaxillae are fused together, forming a single bone. They are  
456 connected through the whole medial margin of the pars dentalis and half of the alary process. The  
457 premaxilla is as long as or slightly shorter than high. The dorsal halves of the alary processes end  
458 with a semicircular tip and point dorsolaterally, getting far from each other. In anterior view, the  
459 dorsal half of the pars dentalis is rough, with five to 17 foramina; in MDHC 18, MDHC 86, MDHC  
460 357, and MDHC 491 the surface is sculptured, with irregular pits and ridges. There is a large foramen  
461 located at the meeting point of the partes dentalis of the left and right premaxillae. In anterior view,  
462 the rectangular pars dentalis is as thick as the alary process and it curves posterolaterally. In posterior  
463 view, the left pars dentalis of MDHC 38, and the right partes dentalis of both MDHC 85 and MDHC

464 87 show one foramen. In the same view, MDHC 357 shows numerous smaller pedicellate pleurodont  
465 teeth, that are not properly aligned in a row, probably for an aberrant condition. In anterior view, the  
466 margo maxillaris is vertical. The margo vomeropalatinum is straight in dorsal view. Between the alary  
467 process and the pars palatina, one to three foramina or an anterior cavity can be found; in this latter  
468 case, dorsally to the cavity there is another smaller one. In posterior view, the pars palatina is smooth,  
469 thinner than the pars facialis, and it keeps the same width for all its length, hiding the ventral fourth  
470 of the pars dentalis. The pars palatina is well developed in dorsal direction, being visible in anterior  
471 view too. The pars palatina of the left premaxilla of MDHC 353 shows one foramen.

472 Maxilla (Fig. 5A-D). In lateral view, the pars facialis is weakly to strongly sculptured (with irregular  
473 pits and ridges); the sculpturing in MDHC 18, MDHC 85, MDHC 87, and MDHC 145 is formed  
474 mainly by ridges, with pits (or foramina) rare or absent. In dorsal view, the anterolateral margin of  
475 the right maxilla of MDHC 353 shows a thin ridge that hosts two foramina. The pars facialis extends  
476 along the anterior half of the pars dentalis. In lateral and medial views, the margo anterioris and the  
477 margo orbitalis are irregular. In lateral view, the left pars dentalis of MDHC 85 shows 10 foramina  
478 distributed on a straight line. The posterior sixth of the pars dentalis is toothless, whereas in the  
479 anterior sixth of the bone, the pars dentalis is not present. In medial view, the teeth of MDHC 357 are  
480 not properly aligned in a row, probably as an aberrant condition. The pars palatina runs along the  
481 whole dorsomedial margin of the pars dentalis; it keeps the same width for the anterior half of the  
482 pars dentalis and it narrows at the anterior end, partly participating to the sharp processus maxillaris  
483 anterior, which shows regular margins. The pars facialis extends more anteriorly than the tooth row,  
484 on the processus maxillaris anterior. The pars palatina is pierced by one to eight foramina; however,  
485 in the right maxilla of MDHC 145 and both maxillae of MDHC 357, no foramen is visible. In some  
486 specimens, between the pars palatina and the pars facialis, there are one to five foramina, well visible  
487 in dorsal view. In dorsal view, on the pars dentalis, the right maxilla of MDHC 353 shows seven  
488 foramina positioned in a straight line.

489 Dentary (Fig. 7E-H). The symphysis is semicircular in medial view. Posteriorly, the bone is pointed.  
490 In dorsal view, in MDHC 357, the posterior fourth is curved toward the medial margin, forming a flat  
491 surface, which shows two cavities. The anterior half of the dorsal and ventral margins are fused  
492 together, so that in medial view the incisura dentalis opens only along its posterior half. The canalis  
493 primordialialis of the left dentary of MDHC 18 and MDHC 357 is filled with the ossified Meckel's  
494 cartilage. In dorsal view, between the folded dorsal margin and the crista dentalis, there can be one  
495 (MDHC 85), two (MDHC 299) or three (MDHC 87, MDHC 261) foramina. In medial view, by the  
496 processus coronoideus, the dorsal margin of the bone is completely flat. MDHC 357 shows numerous  
497 smaller pedicellate pleurodont teeth, arranged chaotically on the crista dentalis and between the  
498 regular teeth. In medial view, the processus coronoideus has a parallelogram-like shape, with smooth  
499 edges; on the other hand, the processus is triangular in MDHC 85 and MDHC 87. Dentaries of MDHC  
500 86 have no processus coronoideus.

501 Vomer (Fig. 8T-V). In dorsal view, the body of the vomer has a triangular shape, with a tip facing  
502 anteromedially. In dorsal view, the margo maxillaris forms a continuous convex anterolateral margin.  
503 The body of the vomer develops in posterodorsal direction, where it forms a pointy extension. In  
504 ventral view, the body of the vomer of MDHC 87 shows a cavity on the margin  
505 intervomeropalatinum. The processus vomeropalatinus minor is well developed and pointy. On the  
506 margo intervomeropalatinum, there is a dorsally directed and triangular expansion; the right vomer  
507 of MDHC 85 and both the left vomers of MDHC 299, and MDHC 491 bear a foramen on this  
508 expansion. In ventral view, the dentigerous ridge is straight and elongated. In lateral view, the  
509 dentigerous ridge is straight (or slightly curved). The width of the dentigerous ridge is the same in the  
510 anterior two thirds of its length, whereas the posterior third becomes narrower. The dentigerous ridge  
511 forms an angle of ca. 180° with the margo intervomeropalatinum in ventral and dorsal views. All the  
512 teeth are visible in lateral and dorsal views; however, the anterior fourth of the dentigerous ridge is  
513 shallower in both vomers of MDHC 85, MDHC 86, MDHC 87, MDHC 299, and MDHC 391, as well  
514 as the right vomer of MDHC 145 and MDHC 261, so much so that the teeth are not visible in ventral

515 and lateral views in these specimens. This happens because the lateral margin of the body of the  
516 vomer expands ventrally to cover the dentigerous ridge.

517

518 *Ichthyosaura alpestris*

519 Premaxilla (Fig. 3I-L). The two premaxillae are fused together forming a single bone. They are  
520 connected through the whole medial margin of the pars dentalis and half of the alary process. The  
521 whole premaxilla is as long as or slightly shorter than high. The separated dorsal portions of the alary  
522 processes point dorsolaterally, getting far from each other. The pars dentalis is of the same thickness  
523 as the alary process and it is curved; it bears one foramen at the meeting point of the two alary  
524 processes. MDHC 416 bears two foramina instead, whereas MRSN A82 10 does not bear any  
525 foramen. In anterior view, both partes dentalis of MDHC 416 bear four foramina, positioned in a  
526 straight line; the two lines (one on the right and one on the left premaxillae) are symmetrical. In  
527 anterior view, in MRSN A82 10B, the dorsal half of the pars dentalis bear five foramina, where the  
528 two premaxillae meet. The margo maxillaris is concave. In posterior view, the pars palatina is well  
529 developed dorsoposteriorly, and it is visible also in anterior view. It keeps approximately the same  
530 width for all its length with regular margins.

531 Maxilla (Fig. 5I-L). The pars facialis extends along the anterior half of the crista dentalis. In medial  
532 view, the pars facialis has a smooth surface, except for the presence of one to six foramina. Between  
533 the pars facialis and the pars palatina of the left maxilla of MDHC 352 and the right maxilla of MRSN  
534 A82 10, a large foramen can be seen. In lateral view, the margo anterioris is regular. The teeth portion  
535 that is visible also in anterior and lateral views is more fragile than the one that is adherent to the  
536 crista dentalis. The posterior half of the pars dentalis is toothless. The pars palatina runs along the  
537 whole dorsomedial margin of the pars dentalis, keeping the same width for the anterior half of the  
538 latter; it narrows at the anterior end, partly participating to the sharp processus maxillaris anterior,  
539 which shows regular margins. The pars facialis extends more anteriorly than the tooth row, on the  
540 processus maxillaris anterior. The pars palatina is pierced by two to eight foramina.

541 Dentary (Fig. 7I-L). The symphysis is semicircular in medial view. In medial view, the processus  
542 articularis is as thick as the rest of the bone. Posteriorly, the dentary is rounded. The dorsal and ventral  
543 margins are completely fused together in MDHC 352, whereas in MDHC 416 they are fused for the  
544 anterior half, so that in medial view the incisura dentalis opens only along its posterior half. In medial  
545 view, the processus coronoideus has a triangular shape.

546 Vomer (Fig. 8Z-AB). In dorsal view, the body of the vomer has a triangular shape, with a tip facing  
547 anteromedially. In ventral view, the body of the vomer of MDHC 416 shows numerous little cavities.  
548 In dorsal view, the margo maxillaris is continuously convex. The body of the vomer develops in  
549 posterodorsal direction, forming a pointy extension. The processus vomeropalatinus minor is well  
550 developed and pointy. In ventral view, the margo intervomeroalatinum forms a concavity. Both in  
551 ventral and lateral view, the dentigerous ridge is straight (or slightly curved) and elongated. The  
552 dentigerous ridge forms an angle of ca. 180° with the margo intervomeroalatinum in ventral and  
553 dorsal views. The margo orbitosphenoideum forms an expansion that runs for the two anterior thirds  
554 of the dentigerous ridge; in the last third it ends suddenly. All the teeth are visible in lateral and dorsal  
555 views.

556

557 *Lissotriton vulgaris*

558 Premaxilla (Fig. 3M-P). The two premaxillae are fused together forming a single bone; they are  
559 connected through the whole medial margin of the pars dentalis and two ventral thirds of the alary  
560 process. The left (or right) half of the premaxilla is twice higher than long. The alary process is quite  
561 robust. The dorsal halves of the alary processes point dorsolaterally, getting far from each other. In  
562 anterior view, the dorsal half of the pars dentalis shows numerous little cavities. The pars dentalis is  
563 as thick as the alary process and it is curved. It bears a small foramen at the meeting point of the two  
564 alary processes. In MDHC 135, in the same place, there are two smaller cavities too, whereas in  
565 MDHC 168 and MDHC 260, there are two other smaller foramina. The margo maxillaris is concave.  
566 The pars palatina is well developed dorsoposteriorly, and it is visible also in anterior view. It keeps

567 approximately the same width for all its length with regular margins. In dorsal view, MDHC 133,  
568 MDHC 135, MDHC 168, and MDHC 260 display a foramen between the alary process and the pars  
569 palatina.

570 Maxilla (Fig. 5M-P). The pars facialis extends along the anterior two thirds of the crista dentalis. It  
571 has a smooth surface in medial view, whereas in lateral view it shows a thickening on the posterior  
572 half. In medial view, under this thickening the pars facialis bears either no foramen or one to two  
573 foramina. Both maxillae of MDHC 132 and the right maxilla of MDHC 133 show a cavity on the  
574 medial surface of the pars facialis. Between the pars facialis and the pars palatina, a cavity or a  
575 foramen can be seen. In lateral view, the margo anterioris is irregular. In lateral view, MDHC 132,  
576 MDHC 133, MDHC 135, MDHC 168, and MDHC 259 show numerous cavities positioned in a  
577 straight line on the pars dentalis; other cavities are visible in dorsal view. The teeth are limited to the  
578 anterior half of the crista dentalis. The pars palatina runs along the whole dorsomedial margin of the  
579 pars dentalis. It keeps the same width for the anterior half of the pars dentalis and it narrows at the  
580 anterior end, without meeting the pars facialis, so that the triangular and sharp processus maxillaris  
581 anterior is formed just by the pars facialis. The pars facialis extends more anteriorly than the tooth  
582 row, on the processus maxillaris anterior. The pars palatina is pierced by one to five foramina.

583 Dentary (Fig. 7M-P). The symphysis is semicircular in medial view. The anterior half of the dorsal  
584 and ventral margins are fused together, so that in medial view the incisura dentalis opens only along  
585 its posterior half. In dorsal view, three foramina are hosted between the folded dorsal margin and the  
586 crista dentalis in MDHC 135 and the right dentary of MDHC 259. The processus coronoideus is  
587 completely absent.

588 Vomer (Fig. 8AC-AE). The body of the vomer has a triangular shape, it is smooth on both the dorsal  
589 and ventral surfaces, and it keeps the same thickness throughout; also, it shows a tip facing  
590 anteromedially. It develops in posterodorsal direction, forming a pointy extension. In dorsal view, the  
591 margo maxillaris is continuously convex. On the anterolateral portion of the margo  
592 intervomeropalatinum, a dorsally directed and triangular expansion is present. The processus

593 vomeropalatinus minor is well developed and pointy. In dorsal view, the concavity bounded by the  
594 processus vomeropalatinus minor and the processus vomeropalatinus major shows a thickened  
595 margin. In ventral view, on the medial portion of the margo interovomeropalatinum, there is a shallow  
596 concavity. In the same view, the dentigerous ridge is straight and elongated. The margo  
597 orbitosphenoideum forms a medially directed expansion, which runs for the whole length of the  
598 dentigerous ridge. The dentigerous ridge forms an angle of ca. 180° with the margo  
599 intervomeropalatinum in ventral and dorsal views. In lateral view, the dentigerous ridge is straight  
600 (or slightly curved).

601

602 *Lissotriton italicus*

603 Premaxilla (Fig. 3Q-T). The two premaxillae are fused together forming a single bone. They are  
604 connected through the whole medial margin of the pars dentalis and the ventral half of the alary  
605 process. The whole premaxilla is as long as or slightly shorter than high. The dorsal halves of the  
606 alary processes point dorsolaterally, getting far from each other. In anterior view, the dorsal half of  
607 the pars dentalis shows numerous little cavities, located at the level of the fusion between the two  
608 alary processes. The pars dentalis is as thick as the alary process and is curved; in posterior view, it  
609 bears a small foramen located at the meeting point of the two alary processes. In contrast to this  
610 general condition, however, MDHC 477 and MDHC 482 show no foramina. The margo maxillaris is  
611 straight, with a small lateral tip anteriorly (visible in dorsal view). In posterior view, the pars palatina  
612 is well developed dorsoposteriorly, and it is visible also in anterior view. It keeps approximately the  
613 same width for all its length with regular margins.

614 Maxilla (Fig. 5Q-T). The pars facialis extends along the anterior half of the crista dentalis and it has  
615 a smooth surface in medial view. In lateral view, it is weakly sculptured. Between the pars facialis  
616 and the pars palatina, either a foramen or a cavity can be seen. In lateral view, the margo anterioris  
617 shows a concavity. In medial view, in MDHC 477, the processus maxillaris posterior is medially  
618 directed. In lateral view, the pars dentalis of MDHC 476 and MDHC 477 show numerous cavities

619 positioned in a straight line. The teeth are limited to the anterior half of the crista dentalis. The pars  
620 palatina runs along the whole dorsomedial margin of the pars dentalis and it is pierced by two or three  
621 foramina. It keeps the same width for the anterior half of the pars dentalis, and it forms a triangular  
622 and sharp processus maxillaris anterior. The pars facialis extends more anteriorly than the tooth row,  
623 on the processus maxillaris anterior.

624 Dentary (Fig. 7Q-T). The symphysis is semicircular in medial view. In MDHC 477, the anterior half  
625 of the bone is medially directed, whereas the rest of the bone is straight. The anterior two third (three  
626 fourth for MDHC 477) of the dorsal and ventral margins are fused together, so that in medial view  
627 the incisura dentalis opens only along its posterior half. The processus coronoideus is completely  
628 absent.

629 Vomer (Fig. 8AF-AH). The body of the vomer develops in posterodorsal direction, forming a pointy  
630 extension; it also has a triangular shape, with a tip facing anteromedially. In dorsal view the margo  
631 maxillaris is continuously convex. On the anterolateral portion of the margo intervomeropalatinum a  
632 dorsally directed triangular expansion is present. The processus vomeropalatinus minor is well  
633 developed and rounded. In dorsal view, the cavity in the middle of the margo choanalis presents a  
634 thicker margin. In ventral view, on the medial portion of the margo interovomeropalatinum, there is  
635 a shallow concavity. In the same view, the dentigerous ridge is straight and elongated. This ridge  
636 forms an angle of ca. 180° with the margo intervomeropalatinum in ventral and dorsal views. In lateral  
637 view, the dentigerous ridge is straight (or slightly curved). The margo orbitosphenoideum forms a  
638 medially directed expansion, which runs for the whole length of the dentigerous ridge.

639

#### 640 *Comparative and phylogenetic analysis*

641 The teeth number for each element of each specimen is reported in Table S3. Concerning the  
642 phylogenetic analysis, as a result of the New Technology Search on the matrix with the 33 dentigerous  
643 bones characters, seven trees were retained, and six trees after the subsequent round of tree bisection  
644 and reconnection. The strict consensus of these latter six trees is figured in Figure 9. The Consistency

645 Index (CI) is 0.89; the Retention Index (RI) is 0.914. The consensus tree displays seven nodes,  
646 excluding the one from which the outgroup diverges from the other clades, and a polytomy at the  
647 base of a clade grouping all members of Pleurodelinae and *Salamandrina*. *Salamandra* and  
648 *Speleomantes* are subsequent sister taxa of the clade including Pleurodelinae and *Salamandrina*.

649

650

## DISCUSSION

651 *Diagnostic characters*

652 Diagnostic characters for each group are provided below and the most important diagnostic characters  
653 at genus level are reported in Table S4. The diagnostic characters reach the taxonomic level that was  
654 possible to achieve based on the data available for the study. Thus, in few cases the diagnostic  
655 characters allow identification to species, whereas in most cases they provide information at the genus  
656 level only. The dentary was revealed not to be highly diagnostic, so that the family was the only level  
657 possible to achieve in most cases, except for *Salamandrina* (see below). Characters for which the  
658 diagnostic value is uncertain (because of the limited number of available specimens) are highlighted  
659 with an asterisk.

660

661 Family Plethodontidae (monogeneric family in Europe so the diagnostic characters of the genus are  
662 valid also for the family)

663 *Speleomantes*

664 Premaxilla. Three times higher than long. Alary process particularly long and slender. Medial margin  
665 of ventral half of premaxilla without any thickening. Pars palatina developed in posterior direction,  
666 not visible in anterior view. Pars palatina subtriangular in shape, enlarging posterolaterally. Alary  
667 process of *S. ambrosii* with expansion extending along its dorsal half, not visible in anterior and  
668 posterior views\*.

669 Maxilla. Whole length of pars dentalis with teeth, including processus maxillaris anterior. Pars  
670 palatina very small, with same width for almost its entire length. Processus maxillaris anterior absent

671 (same in hynobiids). Pars facialis ending more posteriorly than anterior end of tooth row (same in  
672 hynobiids). No sculpturing in lateral view (same in hynobiids).

673 Dentary. Margin fused in anterior two thirds. Symphysis with dorsal bulge. Processus coronoideus  
674 generally absent in *S. italicus*\*

675 Vomer. Concavity bounded by processus vomeropalatinus major and dentigerous ridge (same in  
676 hynobiids). Posteriorly curved dentigerous ridge in ventral view. Angle between dentigerous ridge  
677 and margo intervomeropalatinum less than 90° (same in hynobiids).

678

679 Family Salamandridae

680 Alary process of premaxilla rather short, and premaxilla with curved pars dentalis. Pars palatina  
681 generally visible in anterior view (either poorly developed or well developed; in *S. lanzai*, not visible  
682 in anterior view). Processus maxillaris anterior of maxilla present, pars facialis ends together with  
683 tooth row or more anteriorly (pars facialis participating or not significantly to processus maxillaris  
684 anterior). Dentary symphysis with semicircular shape (same in hynobiids). Concavity on vomer  
685 bounded by processus vomeropalatinus major and variably developed processus vomeropalatinus  
686 minor.

687

688 *Salamandra*

689 Premaxilla. Dorsal margin of pars dentalis forming thin ridge. Same width of pars palatina in all its  
690 length, except for midlength, where it widens and forms a triangular expansion. Dorsal margin of  
691 the pars dentalis and alary process forming anterior concavity (same in hynobiids). *Salamandra*  
692 *salamandra* shows two or three triangular medial expansions on pars dentalis. Pars palatina of *S.*  
693 *lanzai* extremely small and cannot be seen in anterior view.

694 Maxilla. Pars facialis extended posteriorly to first third of pars dentalis. Posterior fourth to fifth of  
695 pars dentalis toothless. Pars palatina with medial triangular expansion with irregular margins (same  
696 in hynobiids). Processus maxillaris anterior formed mainly by pars palatina.

697 Vomer. Angle between dentigerous ridge and margo intervomeropalatinum ca. 130°. Sigmoid  
698 curvature of dentigerous ridge in ventral view. *Salamandra salamandra* shows two concavities on  
699 margo choanalis. Processus vomeropalatinus minor of *S. salamandra* small and pointy.

700

701 *Salamandrina*

702 Premaxilla. Medial margin of alary process thickened. Pars palatina medially enlarging.

703 Maxilla. Pars facialis posteriorly extended to first third of pars dentalis. Processus maxillaris posterior  
704 thick and dorsoventrally expanded. Anterior fourth of pars dentalis is toothed. Pars palatina runs along  
705 anterior third of dorsomedial margin of pars dentalis. Pars palatina semicircular (enlarging anteriorly  
706 and posteriorly) with irregular margins. Posterior half of pars dentalis dorsally curved. In all  
707 specimens of *S. perspicillata*, dorsal half of pars facialis shows triangular medial expansion,  
708 developed in mediodorsal direction and not visible in lateral view. Same expansion in two specimens  
709 of *S. terdigitata* posterodorsally directed, visible also in lateral view. Giving reduced sample (only  
710 eight specimens of *S. perspicillata* and four of *S. terdigitata* have been analysed), more in-depth study  
711 needed to confirm or refute diagnostic potential of this character.

712 Dentary. Dorsal and ventral margins completely fused or nearly so.

713 Vomer. Pars facialis hammer shaped. In lateral view, margo intervomeropalatinum forming small  
714 rounded dorsal expansion.

715

716 Subfamily Pleurodelinae

717 Premaxilla fused, with pars palatina with same width for all its length. Maxilla with processus  
718 maxillaris posterior pointy and thin, pars palatina with same width for anterior half of pars dentalis.  
719 Vomer with straight (or slightly curved) dentigerous ridge, margo intervomeropalatinum forming  
720 triangular dorsal expansion in lateral view (except for *Ichthyosaura*, in which more rounded than  
721 triangular). Extension of body of the vomer pointed.

722

723 *Euproctus platycephalus*\* (only Italian species in the genus, so the diagnostic characters of the  
724 species are valid also for the genus).

725 Premaxilla. Dorsal halves of alary process remain close along all their length. Weakly sculptured in  
726 anterior view.

727 Maxilla. Sculptured in lateral view. Less than posterior sixth of pars dentalis toothless (same in  
728 hynobiids). Combination of processus maxillaris posterior pointy and thin and processus maxillaris  
729 anterior formed mainly by pars facialis.

730 Vomer. Combination of processus vomeropalatinus minor poorly developed and margo  
731 intervomeropalatinum flat in lateral view.

732

733 *Triturus carnifex* (the only Italian species of the genus, so the diagnostic characters of the species  
734 are valid also for the genus).

735 Premaxilla. Sculptured in anterior view.

736 Maxilla. Posterior sixth of pars dentalis toothless.

737 Vomer. Combination of processus vomeropalatinus minor well developed and pointed and margo  
738 intervomeropalatinum flat in lateral view.

739

740 *Ichthyosaura alpestris* (the only extant species in the genus, so the diagnostic characters of the  
741 species are valid also for the genus).

742 Premaxilla. Anterior margin of pars dentalis regular in dorsal view and rather trapezoidal in shape.

743 Maxilla. Combination of posterior half of pars dentalis toothless and processus maxillaris anterior  
744 formed by pars facialis and part of pars palatina.

745 Vomer. Combination of margo intervomeropalatinum forming small rounded dorsal expansion in  
746 lateral view and processus vomeropalatinus minor well developed and pointed.

747

748 *Lissotriton*

749 Premaxilla. Anterior margin of pars dentalis irregular in dorsal view and rather semicircular in  
750 shape. Premaxillae of *L. vulgaris* fused along whole medial margin of pars dentalis and two ventral  
751 thirds of alary process. Left (or right) half of premaxilla of *L. vulgaris* twice higher than long.

752 Maxilla. Combination of pars facialis extended to midlength of pars dentalis and pars palatina runs  
753 along anterior third of dorsomedial margin of pars dentalis. *Lissotriton italicus* weakly sculptured in  
754 lateral view, whereas *L. vulgaris* not sculptured. In *L. italicus*, processus maxillaris anterior formed  
755 by pars facialis and part of pars palatina.

756 Vomer. Margo intervomeropalatinum bearing shallow concavity, with ticker margin in dorsal view.  
757 Margo orbitosphenoideum of *L. italicus* forms expansion medially directed that runs for whole length  
758 of dentigerous ridge. Processus vomeropalatinus minor of *L. italicus* well developed and rounded.

759

#### 760 *Dichotomous key for identifications*

761 Thanks to the diagnostic characters identified above, it has been possible to build a dichotomous key  
762 for the identification of the Italian urodele taxa. In few cases the identification reaches the species  
763 level, whereas in most cases it stops at the genus level. Characters that need to be confirmed with the  
764 study of a higher number of specimens are highlighted with an asterisk.

#### 765 Premaxilla

766 1. Not Fused ..... 2

767 - Fused ..... 7

768 2. The pars palatina develops for the whole ventral half of the alary process, so that the posterior  
769 half of the alary process is not visible in posterior view ..... *Salamandrina* spp.

770 - The pars palatina develops posterodorsally, but the posterior half of the alary process is visible in  
771 posterior view ..... 3

772 3. The premaxilla is as long as or slightly shorter than high ..... 4 (*Salamandra* spp.)

773 - The premaxilla is three times higher than long ..... 6 (*Speleomantes* spp.)

774	4. In posterior view, on the ventral half of the alary process, the medial margin can form two or	
775	three triangular expansions .....	<i>Salamandra salamandra</i>
776	- The alary process is thin, dorsally elongated and ends abruptly .....	5
777	5. The pars palatina is extremely small and cannot be seen in anterior view .....	<i>Salamandra lanzai</i>
778	- The pars palatina is poorly developed but can be seen in anterior view .....	<i>Salamandra atra</i> *
779	6. In lateral view, the alary process shows an expansion that extends along its dorsal half, not visible	
780	in anterior and posterior views .....	<i>Speleomantes ambrosii</i> *
781	- In anterior and posterior views, the alary process shows an expansion laterally directed that	
782	extends along its dorsal half .....	<i>Speleomantes strinatii</i> *
783	7. The dorsal portions of the alary processes remain close to each other along all their length	
784	.....	<i>Euproctus platycephalus</i>
785	- The dorsal portions of the alary processes point dorsolaterally, getting far from each other .....	8
786	8. Ventral half of the alary process sculptured, with irregular pits and ridges .....	<i>Triturus carnifex</i>
787	- Ventral half of the alary process smooth or with a few foramina or cavities .....	9
788	9. Anterior margin of the pars dentalis smooth and regular in posterior view and rather trapezoidal	
789	in shape .....	<i>Ichthyosaura alpestris</i>
790	- Anterior margin of the pars dentalis irregular in posterior view and rather semicircular in shape	
791	.....	10 ( <i>Lissotriton</i> spp.)
792	10. Left (or right) half of the premaxilla twice higher than long .....	<i>Lissotriton vulgaris</i>
793	- Premaxilla is as long as or slightly shorter than high .....	<i>Lissotriton italicus</i>
794	<u>Maxilla</u>	
795	1. The posterior end of the pars dentalis is dorsally curved .....	<i>Salamandrina</i> spp.
796	- The pars dentalis is straight .....	2
797	2. The teeth run for the whole length of the pars dentalis, including the processus maxillaris	
798	anterior. As such, the pars facialis does not reach the anterior end of the tooth row	
799	.....	<i>Speleomantes</i> spp.

800	- The pars facialis does not significantly extend on the processus maxillaris anterior, but it ends	
801	together with the tooth row anteriorly or the pars facialis extends more anteriorly than the tooth	
802	row, on the processus maxillaris anterior .....	3
803	3. The pars facialis does not significantly extend on the processus maxillaris anterior, but it ends	
804	together with the tooth row anteriorly .....	4 ( <i>Salamandra</i> spp.)
805	- The pars facialis extends more anteriorly than the tooth row, on the processus maxillaris anterior	
806	.....	6
807	4. The posterior fifth of the length of the pars dentalis is toothless .....	<i>Salamandra atra</i> *
808	- The posterior fourth of the length of the pars dentalis is toothless .....	5
809	5. The pars facialis extends along the anterior third of the pars dentalis .....	<i>Salamandra salamandra</i>
810	- The pars facialis extends along the anterior half of the pars dentalis .....	<i>Salamandra lanzai</i>
811	6. The pars palatina keeps the same width for the anterior half of the pars dentalis; it narrows at the	
812	anterior end, partly participating to the sharp processus maxillaris anterior, with regular margins	
813	.....	<i>Triturus carnifex</i>
814	- The pars palatina has the same width for almost its entire length; it either ends anteriorly in a flat,	
815	abrupt processus maxillaris anterior, with regular margins, or the pars palatina is subtriangular in	
816	shape, enlarging posterolaterally, or it has the same width for all his length except a widening at	
817	midlength .....	7
818	7. No sculpturing on the pars facialis .....	8
819	- Pars facialis sculptured in lateral view, with irregular pits and ridges .....	9
820	8. Pars facialis extended for more than half of the pars dentalis .....	<i>Ichthyosaura alpestris</i>
821	- Pars facialis extended for half of the pars dentalis or less .....	<i>Lissotriton vulgaris</i>
822	9. Processus maxillaris anterior formed just by the pars facialis .....	<i>Euproctus platycephalus</i>
823	- Processus maxillaris anterior formed by the pars palatina and the pars facialis ..	<i>Lissotriton italicus</i>
824	<u>Vomer</u>	
825	1. In dorsal view, body of the vomer hammer shaped (see description above) ....	<i>Salamandrina</i> spp.

826	- In dorsal view, body of the vomer triangular .....	2
827	2. Processus vomeropalatinus minor is pointed and slender .....	<i>Salamandra salamandra</i>
828	- Processus vomeropalatinus minor poorly or well developed and pointed or well developed and	
829	rounded .....	3
830	3. The dentigerous ridge forms an angle of ca. 130° with the margo intervomeropalatinum	
831	.....	<i>Salamandra</i> spp.
832	- The dentigerous ridge forms an angle of ca. 90° or ca. 180° with the margo intervomeropalatinum	
833	.....	4
834	4. The dentigerous ridge is mediolaterally directed, slightly posteriorly curved, forming with the	
835	margo intervomeropalatinum an angle of less than 90° .....	<i>Speleomantes</i> spp.
836	- The dentigerous ridge forms an angle of ca. 180° with the margo intervomeropalatinum .....	5
837	5. The processus vomeropalatinus minor is poorly developed .....	<i>Euproctus platycephalus</i>
838	- The processus vomeropalatinus minor is well developed .....	6
839	6. On the margo intervomeropalatinum there is a triangular expansion dorsally directed .....	7
840	- On the margo intervomeropalatinum there is a deep concavity or the margo intervomeropalatinum	
841	is straight .....	<i>Ichthyosaura alpestris</i>
842	7. Processus vomeropalatinus minor rounded .....	<i>Lissotriton italicus</i>
843	- Processus vomeropalatinus minor forming a tip .....	8
844	8. Processus vomeropalatinus major particularly extended, giving the body of the vomer a	
845	trapezoidal shape .....	<i>Triturus carnifex</i>
846	- Processus vomeropalatinus major short, giving the body of the vomer a rectangular shape	
847	.....	<i>Lissotriton vulgaris</i>
848	<u>Dentary</u>	
849	1. The symphysis shows a dorsal bulge in medial view .....	<i>Speleomantes</i> spp.
850	- The symphysis is semicircular .....	2
851	2. Dorsal and ventral margins fused for at least the anterior five sixths .....	<i>Salamandrina</i> spp.

852 - Dorsal and ventral margins unfused or fused for the anterior half or the anterior two third or less  
853 ..... Pleurodelinae / *Salamandra* spp.

854

855 *Variation in the number of tooth positions*

856 Urodeles (like most lissamphibians) have small and somehow delicate teeth that are attached to the  
857 inner side of the jaws (a condition called pleurodonty). Adult teeth usually have a zone of weakness,  
858 formed by fibrous, poorly mineralized tissue, giving sufficient flexibility to permit the crown to bent  
859 inwards into the oral cavity. This condition results from a developmental peculiarity of  
860 lissamphibians: the base of the tooth (pedicel of dentine) and its enamel-covered crown mineralize  
861 from separate centres and fail to fuse during tooth formation. This state is called pedicely (Schoch,  
862 2014). As such, the number of teeth can be counted based on the number of pedicels (in other words,  
863 tooth positions) even though the crown is broken and lost, as it is the case in most of both dry-skeleton  
864 specimens and fossils. In general, the number of tooth positions is a character of uncertain value, as  
865 it increases during larval and adult life (Deban et al., 2000). However, through the data collected  
866 herein some consideration can be done. The number of teeth on the premaxilla (Figure 10A) allows  
867 for the distinction of the genus *Speleomantes* (with a mean of four tooth position for *S. ambrosii* and  
868 *S. strinatii*; the studied specimen of *S. italicus* does not preserve a premaxilla) and Salamandridae.  
869 *Salamandra* (with a mean of 22 tooth position for *S. lanzai*, 19 for *S. atra*, and 25 for *S. salamandra*)  
870 is also distinguishable from the subfamily Pleurodelinae (with a mean ranging from eight to 14 for  
871 the different genera). Among this latter clade, it is not possible to identify single genera based on  
872 teeth number. Similarly, *Salamandrina* has a small difference in the mean number of teeth in the  
873 premaxilla compared to the Pleurodelinae, but the difference is so small that it should not be  
874 considered as a possibly diagnostic character, given that the maximum number of teeth of  
875 *Salamandrina* overlaps with the minima of Pleurodelinae. As such, it seems that the number of teeth  
876 in the premaxilla can be a somehow reliable diagnostic character to distinguish *Salamandra* and  
877 *Speleomantes* from each other and from Pleurodelinae and *Salamandrina*. However, these three major

878 groups can be already separated using many other diagnostic characters as seen above. Despite not  
879 being important for the diagnoses at species level, it seems that the number of teeth in the premaxilla  
880 possesses a quite significant phylogenetic value, separating taxa that are phylogenetically far and  
881 grouping together taxa that are close.

882 The number of tooth positions on the maxilla (Figure 10B) divides the genera into three major groups  
883 based on average numbers: *Speleomantes*, *Euproctus*, and *Salamandra* (with an average number of  
884 tooth positions ranging from 24 to 36 in the different species of the genera), *Triturus*, *Ichthyosaura*,  
885 and *Lissotriton* (with a mean ranging from 12 to 18), and *Salamandrina* (from nine to 10). As such,  
886 the number of teeth in the maxilla could have a little diagnostic value, but the minimum number of  
887 tooth positions of *Speleomantes* is very close to the maxima of *Ichthyosaura*, *Lissotriton*, and  
888 *Triturus*, and the maximum number of tooth positions of *Salamandrina* overlaps the number of tooth  
889 positions of Pleurodelinae. As such, the number of tooth positions in the maxilla is not significant.  
890 Also, it has not much phylogenetic significance, given that for example *Salamandra* has a similar  
891 number to *Speleomantes* despite being very far phylogenetically from it (belonging to two different  
892 families that are separated by many branches of American and Asian taxa). Similarly, *Euproctus* is  
893 within the range of *Salamandra* and *Speleomantes*, despite belonging to the same subfamily of  
894 *Triturus*, *Lissotriton*, and *Ichthyosaura*.

895 The number of tooth position in the dentary (Figure 10C) shows a similar range in all the genera, only  
896 weakly separating *Salamandra* from the other genera. This makes again the dentary the dentigerous  
897 bone with the most conservative morphology within Italian urodeles. The number of tooth position  
898 of the vomer (Figure 10D) is very variable, and the ranges of all considered salamandrids extensively  
899 overlap. *Speleomantes* has a lower number of teeth, somehow as expected as the morphology of the  
900 vomer is clearly dissimilar and shows a way shorter dentigerous ridge compared to Salamandridae.

901

902 *Intra- and interspecific variation*

903 Some characters observed in the tooth-bearing elements exhibit significantly more variability than  
904 others, like the position and the number of foramina and/or cavities, which are highly-variable intra-  
905 and interspecific characters: in every dentigerous bone there can be a varying number of foramina  
906 and/or depressions, or they can be completely absent. Concerning the margins of the bone, generally,  
907 the margo orbitalis of the maxilla is regular, whereas the margo anterioris is irregular. However, that  
908 is not true for all the species and even interspecifically: for example, in *S. atra* and *S. salamandra*,  
909 the two margins can be different in specimens of the same species. The dentary is particularly devoid  
910 of taxonomic significance in all the genera, even when considering variable identifying characters:  
911 the symphysis is different in *Speleomantes*, where it shows a dorsal bulge, but this character is also  
912 present (to a lesser extent and with a less regular shape) in *Triturus carnifex* MDHC 85. This suggests  
913 that the dorsal bulge could be a highly variable character. Other characters in the dentary, such as the  
914 level of margin fusion, the thickness of the margins, and the general shape of the bone, are consistent  
915 across all species or are not significant, likely linked with different ontogenetic stages. As far as the  
916 vomer is concerned, in most specimens of *Triturus* all the teeth are visible in lateral view, but in some  
917 specimens (e.g. MDHC 261), the teeth are not visible due to the lateral margin of the body of the  
918 vomer expanding to a more ventral level than the dentigerous ridge.

919

## 920 *Phylogenetic analysis*

921 The phylogenetic analysis resulted in a well-supported Salamandridae clade, with *Speleomantes*  
922 excluded from it. The species within the genus *Salamandra* and the genus *Speleomantes* are  
923 monophyletic in the resulting tree. The two species of *Salamandrina* and the two Italian species of  
924 *Lissotriton* are also correctly grouped together. *Salamandra* is the sister group of the clade formed by  
925 *Salamandrina* and all the species of Pleurodelinae. The position of *Salamandrina*, in a polytomy with  
926 Pleurodelinae, is in line with the affinities pointed out by other morphological phylogenetic analyses  
927 (Marjanovic & Witzmann, 2015; Macaluso et al. 2022), but contrary to what is currently concluded  
928 by molecular phylogenetic studies (Zhang et al., 2008; Pyron & Wiens, 2011; Rancilhac et al. 2021).

929 The general morphological affinity between *Salamandrina* and the newts (including several  
930 characters on the dentigerous bones as e.g. the straight dentigerous ridge of the vomer) could be the  
931 result of either shared plesiomorphic characters, which seems more likely at least in the case of the  
932 vertebrae (Macaluso et al. 2022, 2023b), or due to evolutionary convergence.

933

934

## CONCLUSION

935 The present work successfully provides taxonomically significant diagnostic characters at the genus  
936 (and in some cases species) level for the extant Italian urodeles, including some taxa with poorly  
937 studied osteology, such as *Speleomantes* spp. and *Euproctus platycephalus*. Italian urodeles exhibit  
938 rather reliable diagnostic characters on premaxillae, maxillae, and vomers, but not in the dentaries,  
939 for which only the family level can be reached. Some characters are extremely variable, such as the  
940 number and the position of foramina and concavities and the regularity of the margins of the bones.  
941 The phylogenetic analysis based on newly defined characters on the tooth-bearing bones resulted in  
942 the recognition of the well-supported monophyletic Salamandridae and Pleurodelinae. *Salamandrina*  
943 was recovered as part of the Pleurodelinae clade, in agreement with previous phylogenetic analyses  
944 based on morphology, but in contrast with the results of the analyses based on molecular data.

945

946

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954

955

## SUPPLEMENTARY MATERIAL

956 Supplementary material associated with this article can be found at <[http://www-](http://www-9.unipv.it/webshi/appendix/index.html)  
957 [9.unipv.it/webshi/appendix/index.html](http://www-9.unipv.it/webshi/appendix/index.html)> manuscript number 15648

958

959

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CAPTIONS TO FIGURES

1055 **Fig. 1.** Terminology followed for the dentigerous bones. A-D: right premaxilla of *Salamandra atra*  
1056 (MDHC 394) in anterior (A), posterior (B), dorsal (C) and lateral (D) views. Abbreviations: appm  
1057 alary process of the premaxilla; cr. den, crista dentalis; ma. mx, margo maxillaris; ma. vp, margo  
1058 vomeropalatinum; pdpm, pars dentalis of the premaxilla; pppm, pars palatina of the premaxilla; su.  
1059 den, sulcus dentalis. E-F: left maxilla of *Salamandra lanzai* (MDHC 362) in medial (E) and lateral (F)  
1060 views. Abbreviations: cr. den, crista dentalis; ma. a, margo anterioris; ma. nas, margo nasalis; ma.  
1061 orb, margo orbitalis; ma. prf, margo praefrontalis; pdm, pars dentalis of the maxilla; pfm, pars facialis  
1062 of the maxilla; ppm, pars palatina of the premaxilla; pr. mx. a, processus maxillaris anterior; pr. mx.  
1063 p, processus maxillaris posterior; su. den, sulcus dentalis. G-H: left dentary of *Euproctus*  
1064 *platycephalus* (MDHC 507) in medial (G) and ventrolateral (H) views. Abbreviations: can. pr, canalis  
1065 primordialis; cor, processus coronoideus; inc. den, incisura dentalis; pr. art, processus articularis; su.  
1066 den, sulcus dentalis; symp, symphysis. I-K: left vomer of *Salamandra salamandra* (MDHC 205) in  
1067 dorsal (I), lateral (J) and ventral (K) views. Abbreviations: dr, dentigerous ridge; ma. choa, margo  
1068 choanalis; ma. imx, margo intermaxillaris; ma. ivp, margo intervomeropalatinum; ma. mx, margo  
1069 maxillaris; ma. obsph, margo orbitosphenoideum; ma. psph, margo parasphenoideum; pr. maj,  
1070 processus vomeropalatinus major; pr. min, processus vomeropalatinus minor; su. den, sulcus dentalis;  
1071 vb, body of the vomer. Scale bar: 1 mm.

1072 **Fig. 2.** Premaxillae of Italian salamanders. A-D: right premaxilla of *Speleomantes ambrosii* (MDHC  
1073 301) in anterior (A), posterior (B), dorsal (C) and lateral (D) views; E-H: left premaxilla of  
1074 *Speleomantes strinatii* (MDHC 486) in anterior (E), posterior (F), dorsal (G) and lateral (H) views; I-  
1075 L: left premaxilla of *Salamandra lanzai* (MDHC 362) in anterior (I), posterior (J), dorsal (K) and  
1076 lateral (L) views; M-P: right premaxilla of *Salamandra atra* (MDHC 394) in anterior (M), posterior  
1077 (N), dorsal (O) and lateral (P) views; Q-T: left premaxilla of *Salamandra salamandra* (MDHC 205)  
1078 in anterior (Q), posterior (R), dorsal (S) and lateral (T) views; U-X: left premaxilla of *Salamandrina*

1079 *perspicillata* (MDHC 406) in anterior (U), posterior (V), dorsal (W) and lateral (X) views; Y-AB:  
1080 left premaxilla of *Salamandrina terdigitata* (MDHC 333) in anterior (Y), posterior (Z), dorsal (AA)  
1081 and lateral (AB) views. Scale bars: 1 mm.

1082 **Fig. 3.** Premaxillae of Italian newts. A-D: premaxilla of *Triturus carnifex* (MDHC 85) in anterior (A),  
1083 posterior (B), dorsal (C) and left lateral (D) views; E-H: premaxilla of *Euproctus platycephalus*  
1084 (MDHC 507) in anterior (E), posterior (F), dorsal (G) and left lateral (H) views; I-L: premaxilla of  
1085 *Ichthyosaura alpestris* (MDHC 416) in anterior (I), posterior (J), dorsal (K) and left lateral (L) view;  
1086 M-P: premaxilla of *Lissotriton vulgaris* (MDHC 132) in anterior (M), posterior (N), dorsal (O) and  
1087 left lateral (P) views; Q-T: premaxilla of *Lissotriton italicus* (MDHC 482) in anterior (Q), posterior  
1088 (R), dorsal (S) and left lateral (T) views. Scale bars: 1 mm.

1089 **Fig. 4.** Maxillae of Italian salamanders. A-D: right maxilla of *Speleomantes ambrosii* (MDHC 301)  
1090 in medial (A), lateral (B), ventral (C) and dorsal (D) views; E-H: left maxilla of *Speleomantes italicus*  
1091 (MDHC 61) in medial (E), lateral (F), ventral (G) and dorsal (H) views; I-L: left maxilla of  
1092 *Speleomantes strinatii* (MDHC 486) in medial (I), lateral (J), ventral (K) and dorsal (L) views; M-P:  
1093 left maxilla of *Salamandra lanzai* (MDHC 362) in medial (M), lateral (N), ventral (O) and dorsal (P)  
1094 views; Q-T: left maxilla of *Salamandra atra* (MDHC 394) in medial (Q), lateral (R), ventral (S) and  
1095 dorsal (T) views; U-Y: left maxilla of *Salamandra salamandra* (MDHC 205) in medial (U), lateral  
1096 (V), ventral (X) and dorsal (Y) views; Z-AC: right maxilla of *Salamandrina perspicillata* (MDHC  
1097 300) in medial (Z), lateral (AA), ventral (AB) and dorsal (AC) views; AD-AG: left maxilla of  
1098 *Salamandrina terdigitata* (MDHC 333) in medial (AD), lateral (AE), ventral (AF) and dorsal (AG)  
1099 views. Scale bars: 1 mm.

1100 **Fig. 5.** Maxillae of Italian newts. A-D: left maxilla of *Triturus carnifex* (MDHC 38) in medial (A),  
1101 lateral (B), ventral (C) and dorsal (D) views; E-H: left maxilla of *Euproctus platycephalus* (MDHC  
1102 507) in medial (E), lateral (F), ventral (G) and dorsal (H) views; I-L: left maxilla of *Ichthyosaura*  
1103 *alpestris* (MDHC 416) in medial (I), lateral (J), ventral (K) and dorsal (L) views; M-P: left maxilla

1104 of *Lissotriton vulgaris* (MDHC 132) in medial (M), lateral (N), ventral (O) and dorsal (P) views; Q-  
1105 T: left maxilla of *Lissotriton italicus* (MDHC 482) in medial (Q), lateral (R), ventral (S) and dorsal  
1106 (T) views. Scale bars: 1 mm.

1107 **Fig. 6.** Dentaries of Italian salamanders. A-D: left dentary of *Speleomantes ambrosii* (MDHC 301) in  
1108 medial (A), lateral (B), dorsal (C) and ventral (D) views; E-H: left dentary of *Speleomantes italicus*  
1109 (MDHC 61) in medial (E), lateral (F), dorsal (G) and ventral (H) views; I-L: left dentary of  
1110 *Speleomantes strinatii* (MDHC 486) in medial (I), lateral (J), dorsal (K) and ventral (L) views; M-P:  
1111 left dentary of *Salamandra lanzai* (MDHC 362) in medial (M), lateral (N), dorsal (O) and ventral (P)  
1112 views; Q-T: left dentary of *Salamandra atra* (MDHC 394) in medial (Q), lateral (R), dorsal (S) and  
1113 ventral (T) views; U-X: left dentary of *Salamandra salamandra* (MDHC 205) in medial (U), lateral  
1114 (V), dorsal (W) and ventral (X) views; Y-AB: left dentary of *Salamandrina perspicillata* (MDHC  
1115 300) in medial (Y), lateral (Z), dorsal (AA) and ventral (AB) views; AC-AF: right dentary of  
1116 *Salamandrina terdigitata* (MDHC 332) in medial (AC), lateral (AD), dorsal (AE) and ventral (AF)  
1117 views. Scale bars: 1 mm.

1118 **Fig. 7.** Dentaries of Italian newts. A-D: left dentary of *Euproctus platycephalus* (MDHC 507) in  
1119 medial (A), lateral (B), dorsal (C) and ventral (D) views; E-H: left dentary of *Triturus carnifex*  
1120 (MDHC 85) in medial (E), lateral (F), dorsal (G) and ventral (H) views; I-L: left dentary of  
1121 *Ichthyosaura alpestris* (MDHC 416) in medial (I), lateral (J), dorsal (K) and ventral (L) views; M-P:  
1122 left dentary of *Lissotriton vulgaris* (MDHC 132) in medial (M), lateral (N), dorsal (O) and ventral (P)  
1123 views; Q-T: left dentary of *Lissotriton italicus* (MDHC 482) in medial (Q), lateral (R), dorsal (S) and  
1124 ventral (T) views. Scale bars: 1 mm.

1125 **Fig. 8.** Vomers of Italian urodeles. A-C: left vomer of *Speleomantes ambrosii* (MDHC 301) in dorsal  
1126 (A), lateral (B) and medial (C) views; D-F: right vomer of *Speleomantes strinatii* (MDHC 486) in  
1127 dorsal (D), lateral (E) and medial (F) views; G-I: left vomer of *Salamandra lanzai* (MDHC 362) in  
1128 dorsal (G), lateral (H) and medial (I) views; J: left vomer of *Salamandra atra* (MDHC 394B) in

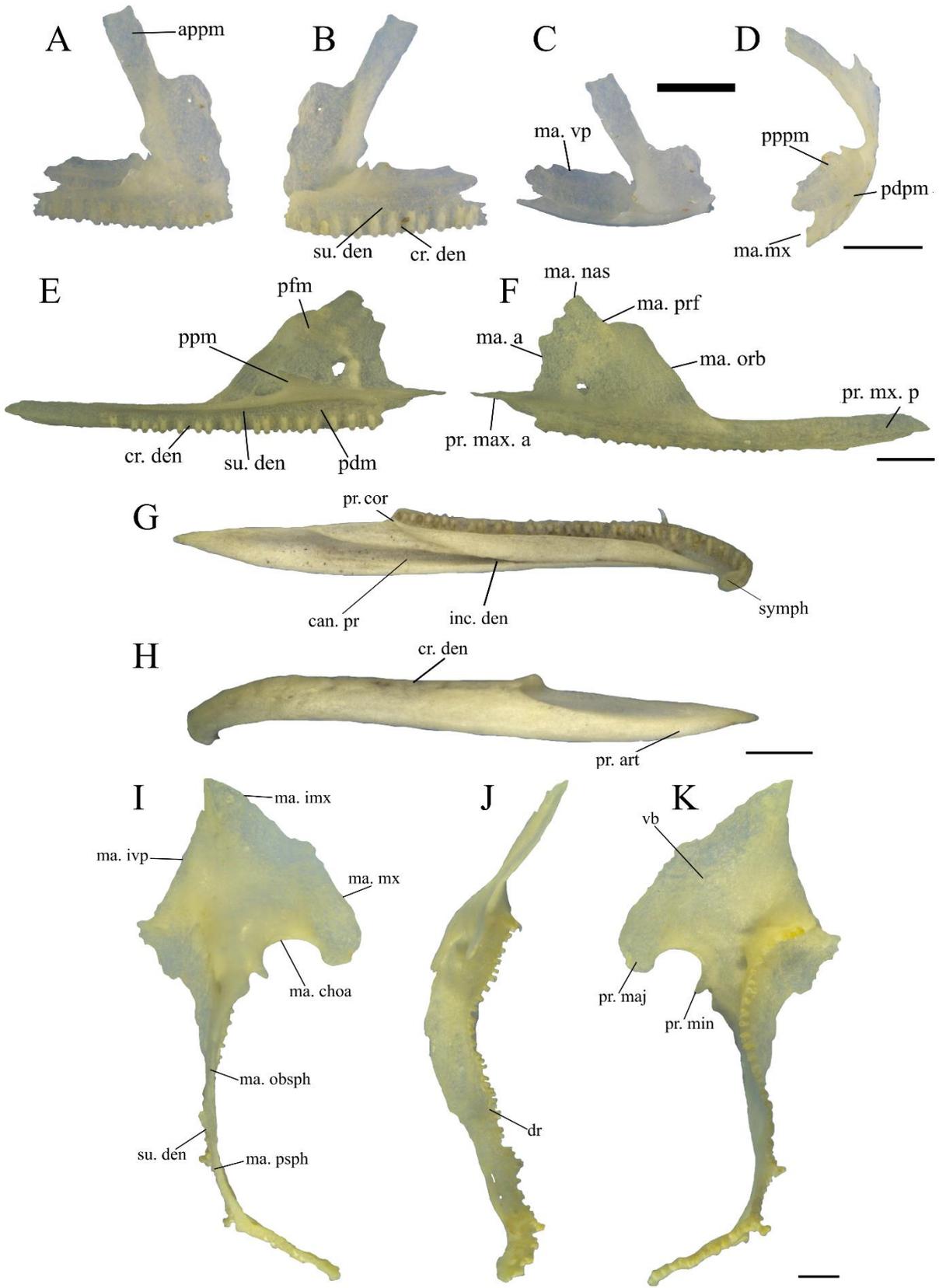
1129 ventral view; K-M: right vomer of *Salamandra salamandra* (MDHC 205) in dorsal (K), lateral (L)  
1130 and medial (M) views; N-P: left vomer of *Salamandrina perspicillata* (MDHC 406) in dorsal (N),  
1131 lateral (O) and medial (P) views; Q-S: right vomer of *Salamandrina terdigitata* (MDHC 332) in dorsal  
1132 (Q), lateral (R) and medial (S) views; T-V: right vomer of *Triturus carnifex* (MDHC 85) in dorsal  
1133 (T), lateral (U) and medial (V) views; W-Y: right vomer of *Euproctus platycephalus* (MDHC 507) in  
1134 dorsal (W), lateral (X) and medial (Y) views; Z-AB: right vomer of *Ichthyosaura alpestris* (MDHC  
1135 416) in dorsal (Z), lateral (AA) and medial (AB) views; AC-AE: right vomer of *Lissotriton vulgaris*  
1136 (MDHC 132) in dorsal (AC), lateral (AD) and medial (AE) views; AF-AH: right vomer of *Lissotriton*  
1137 *italicus* (MDHC 482) in dorsal (AF), lateral (AG) and medial (AH) views. Scale bars: 1 mm.

1138 **Fig. 9.** Consensus tree obtained with a maximum parsimony phylogenetic approach using the matrix  
1139 including the 33 dentigerous bones characters.

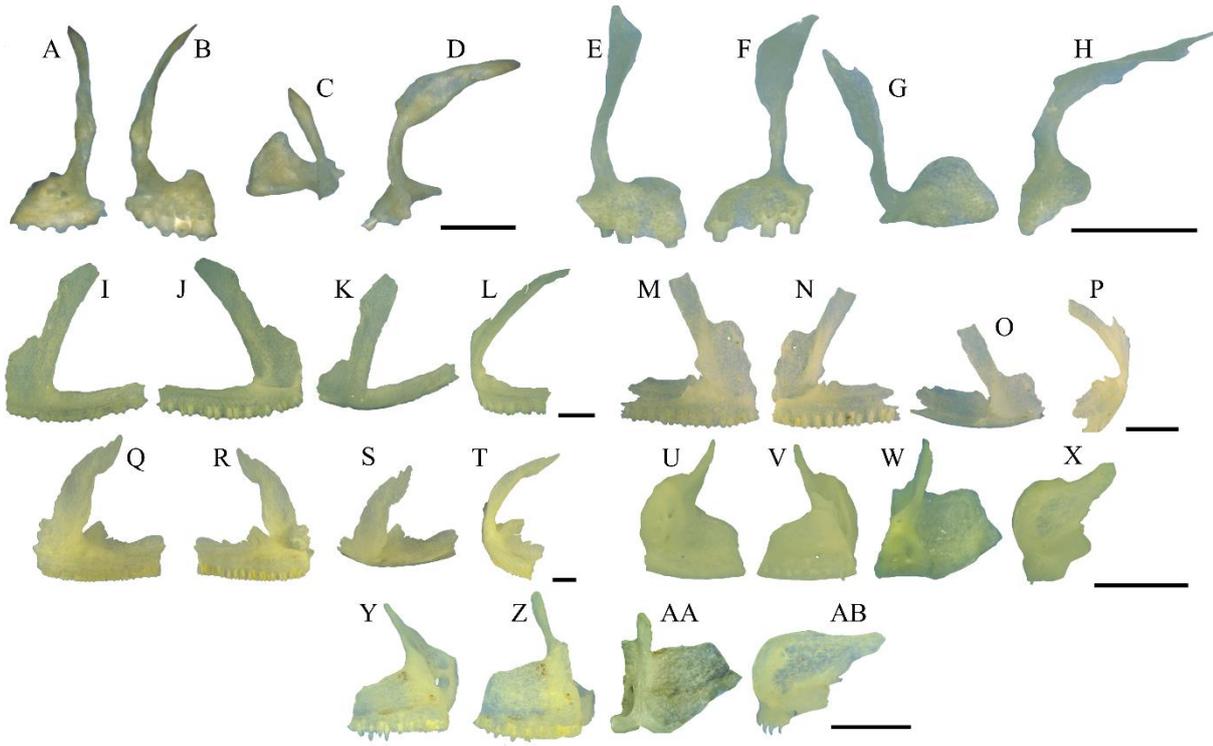
1140 **Fig. 10.** Number of tooth positions in Italian urodele genera. A: tooth positions in the premaxilla at  
1141 the genus level. In the fused ones, half of the premaxilla is considered. B: tooth positions in the  
1142 maxilla at the genus level. C: tooth positions in the dentary at the genus level. D: tooth positions in  
1143 the vomer at the genus level. The graphs are based on the data reported in Table S3.

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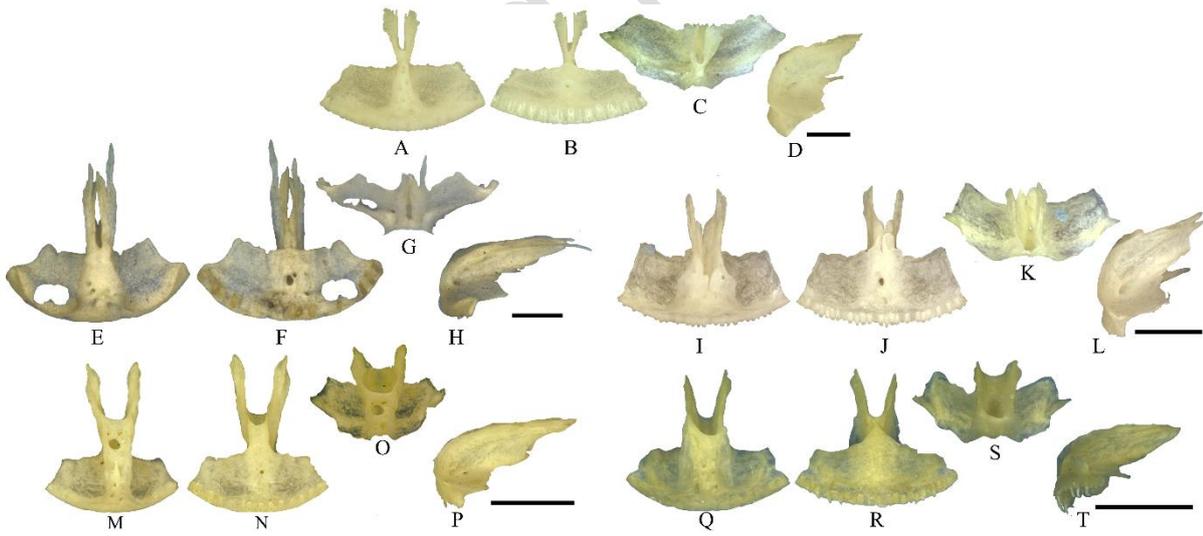
1149 Fig. 2



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1152 Fig. 3

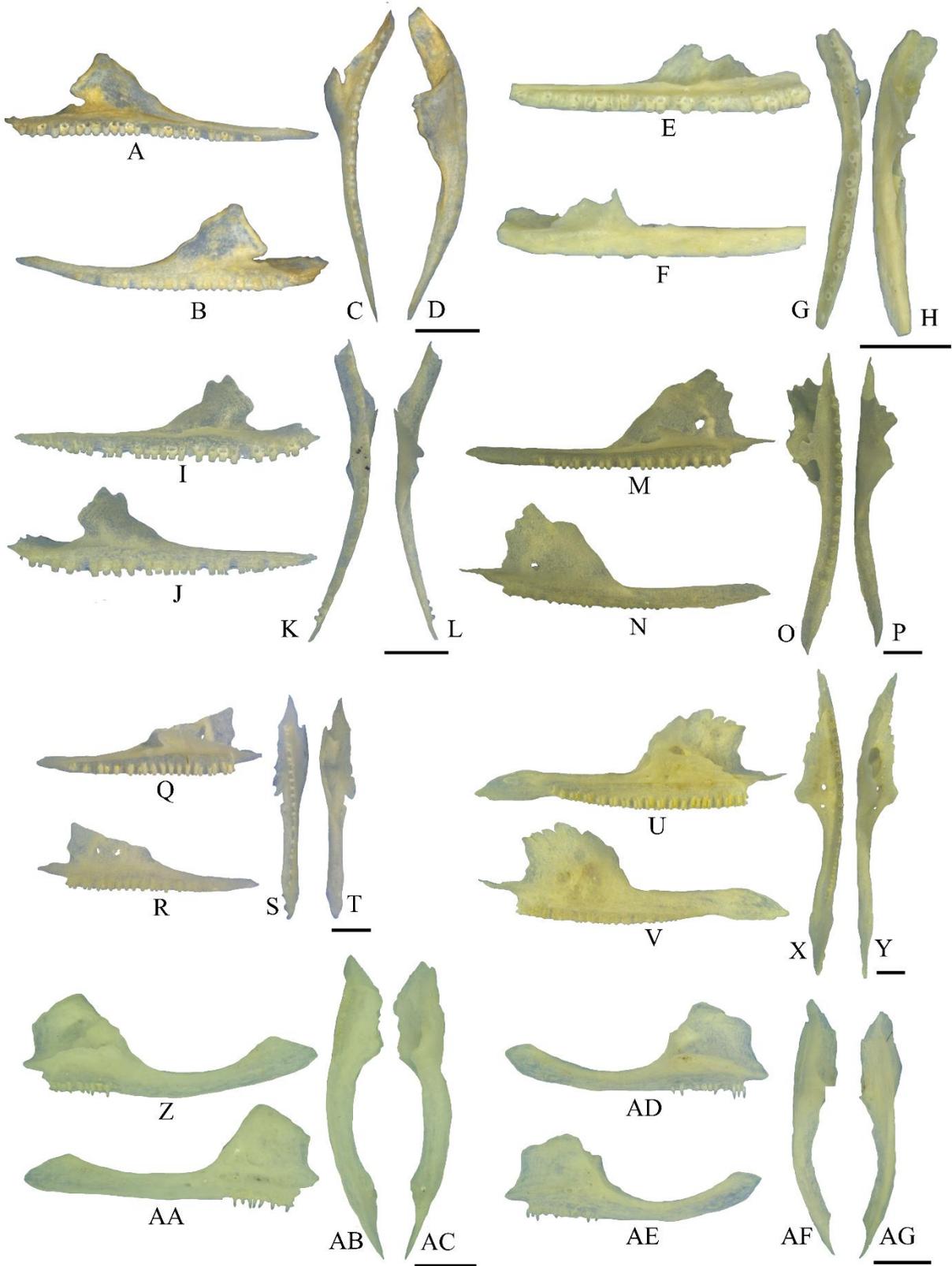


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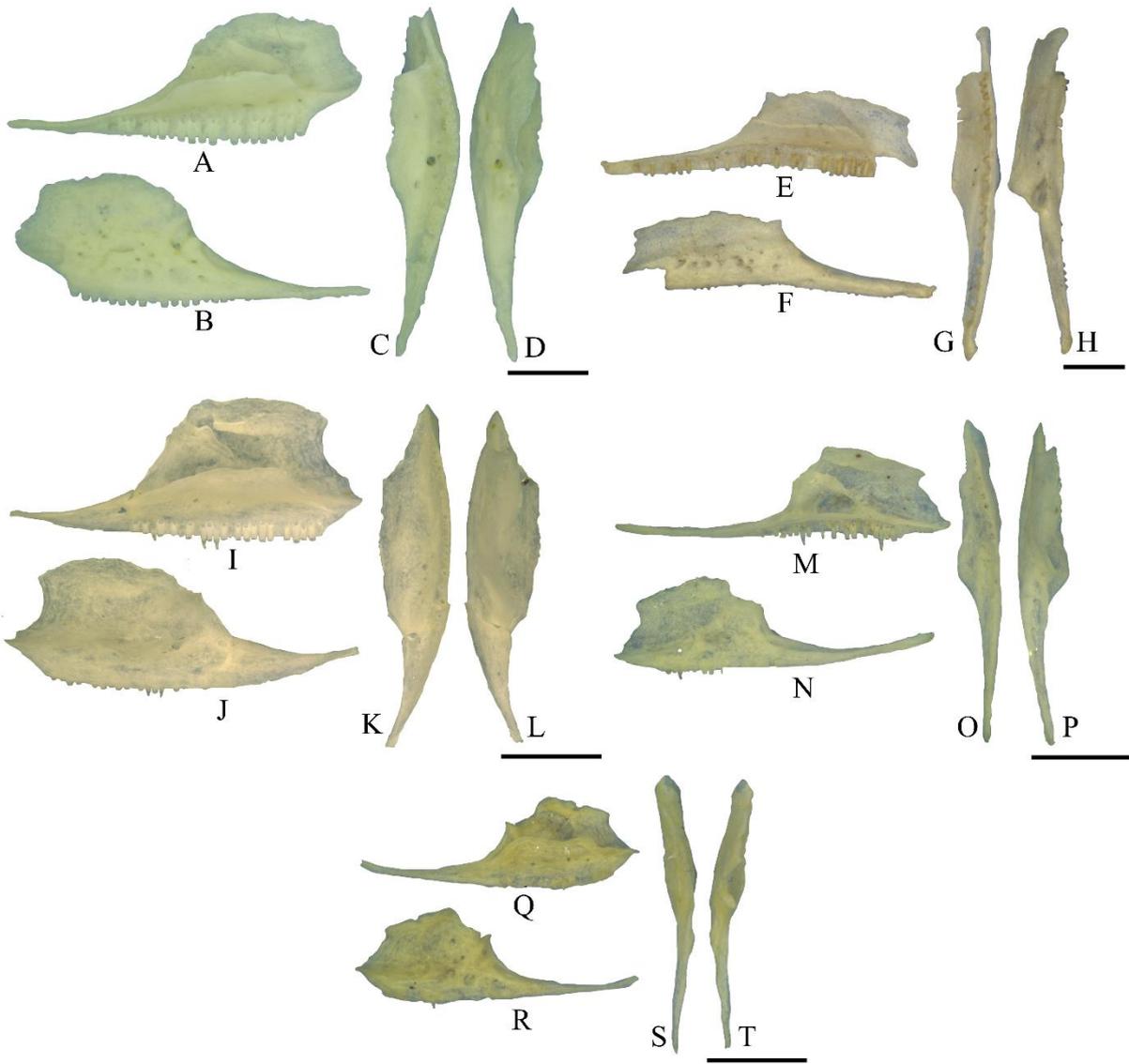
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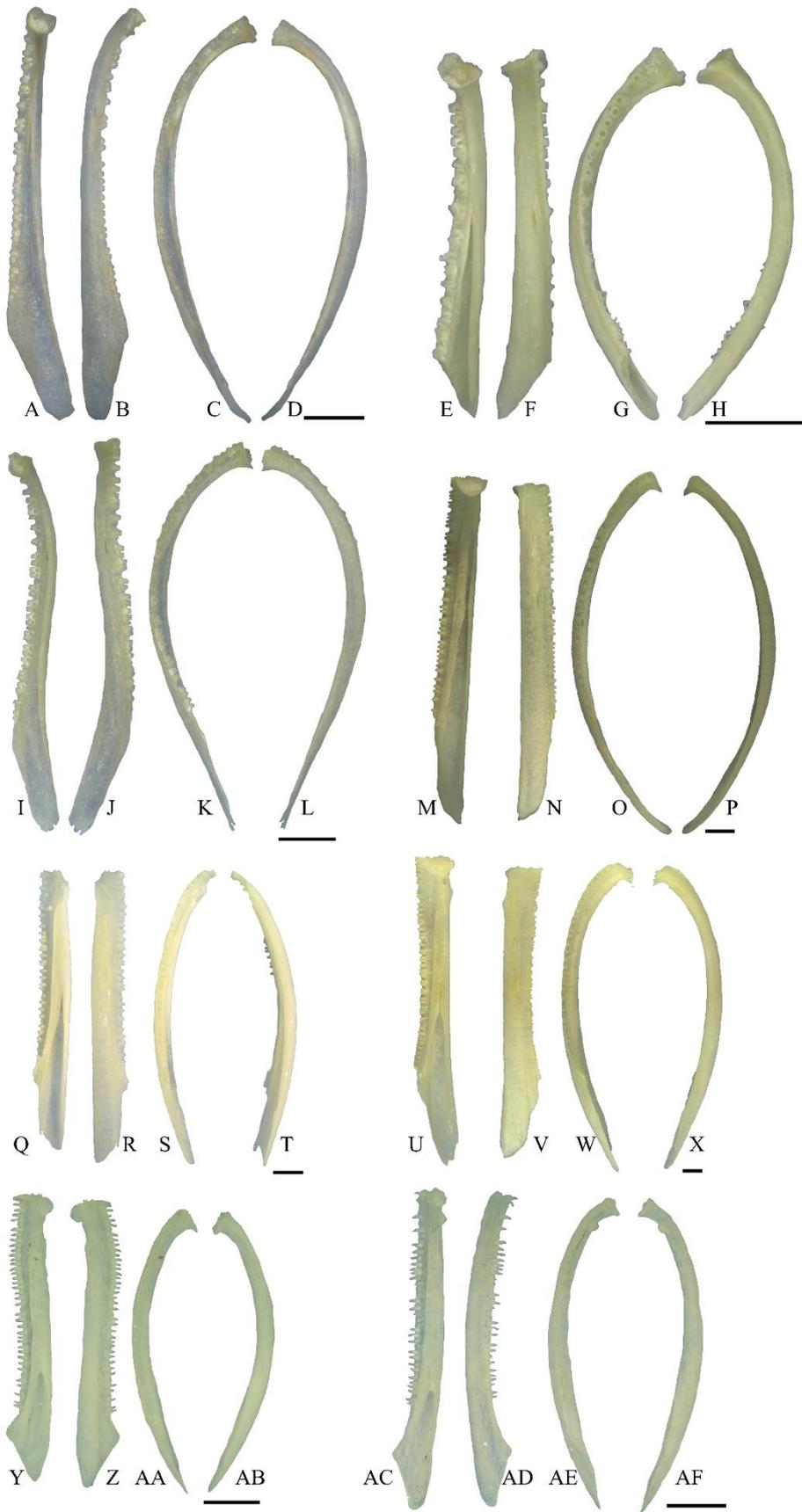


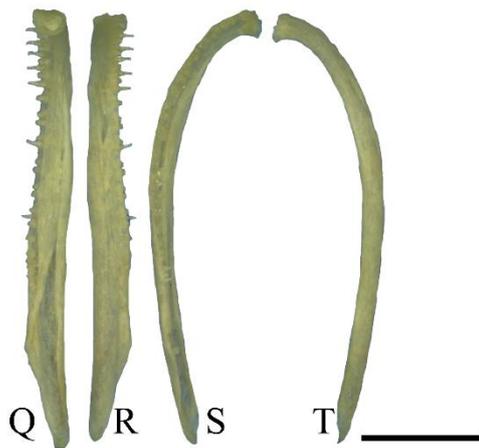
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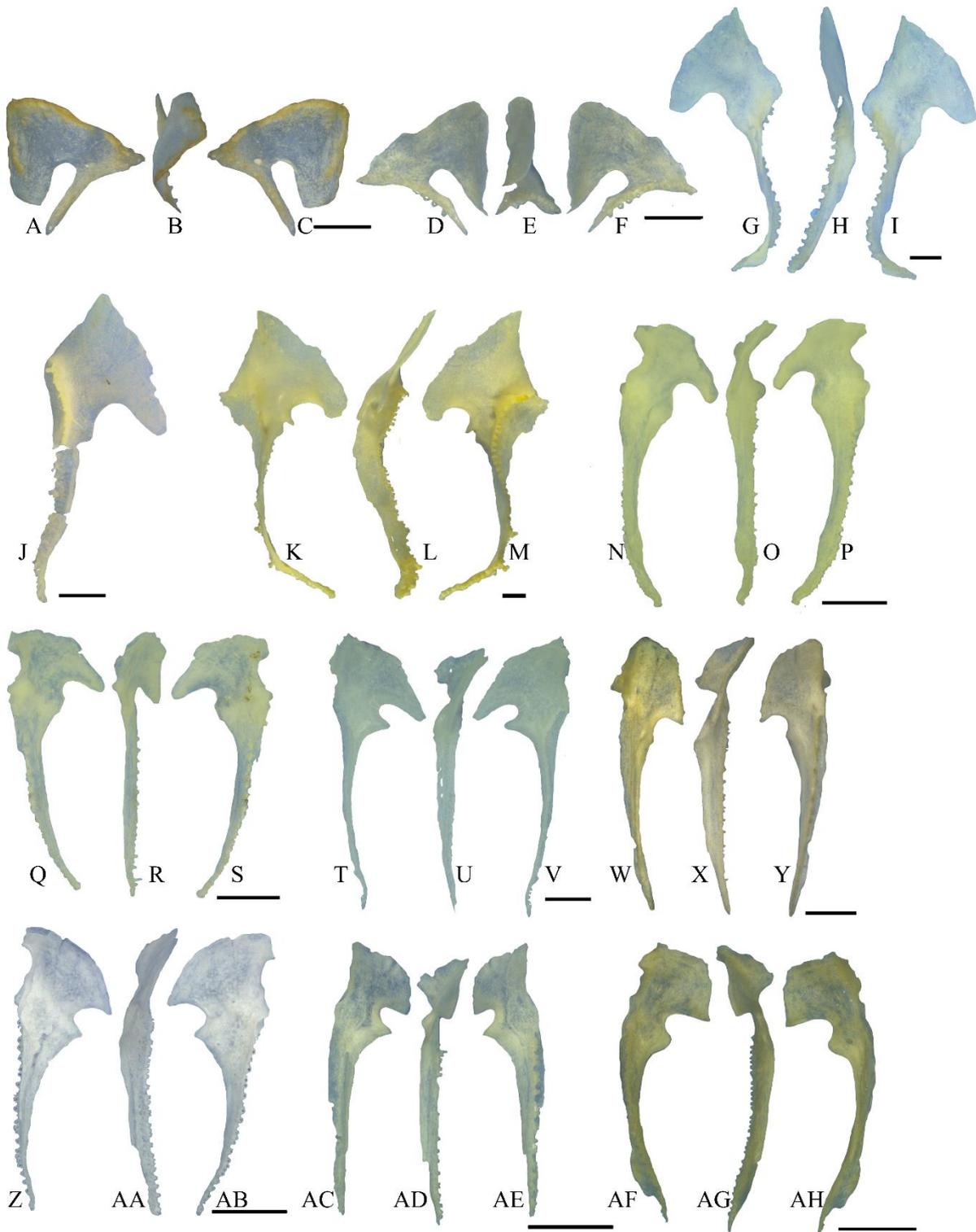
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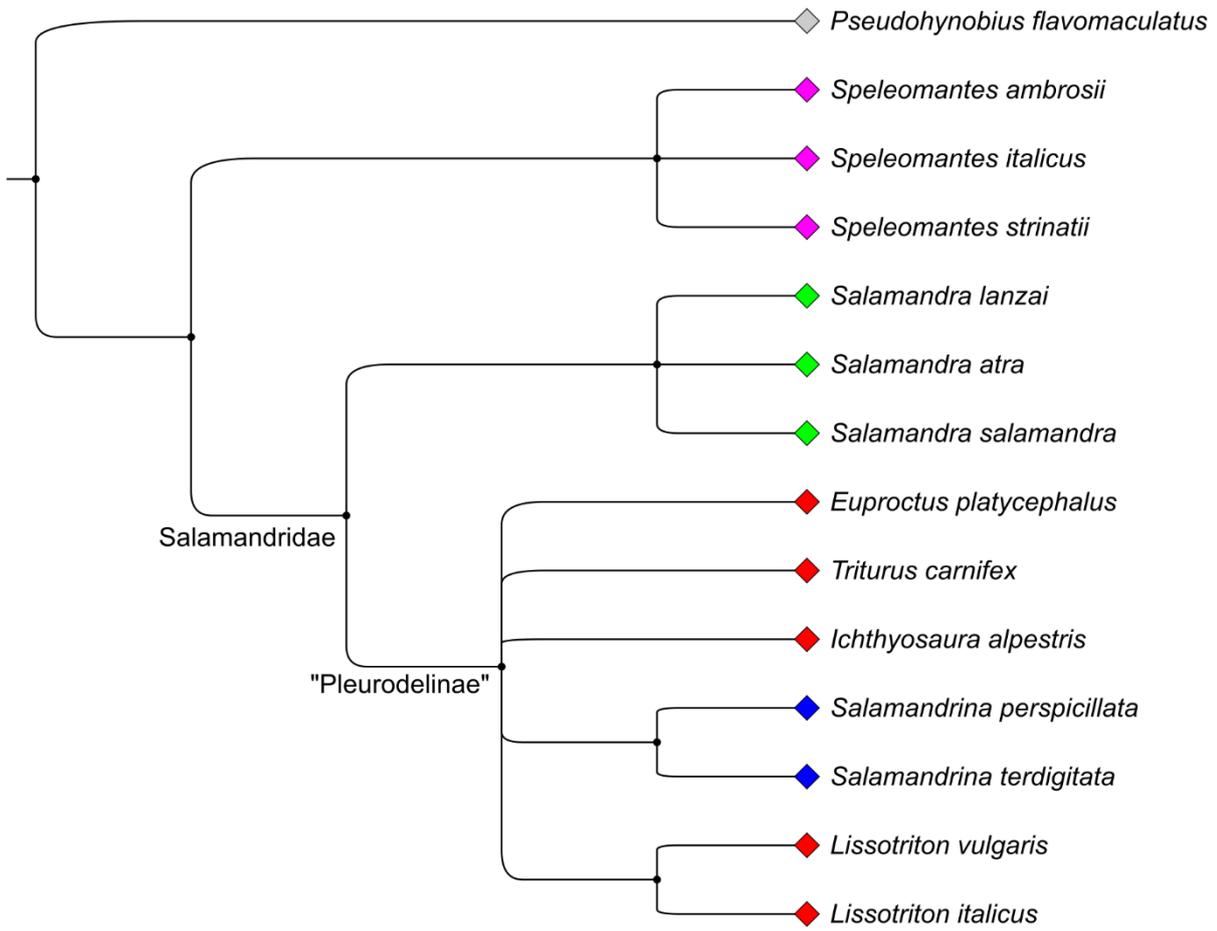






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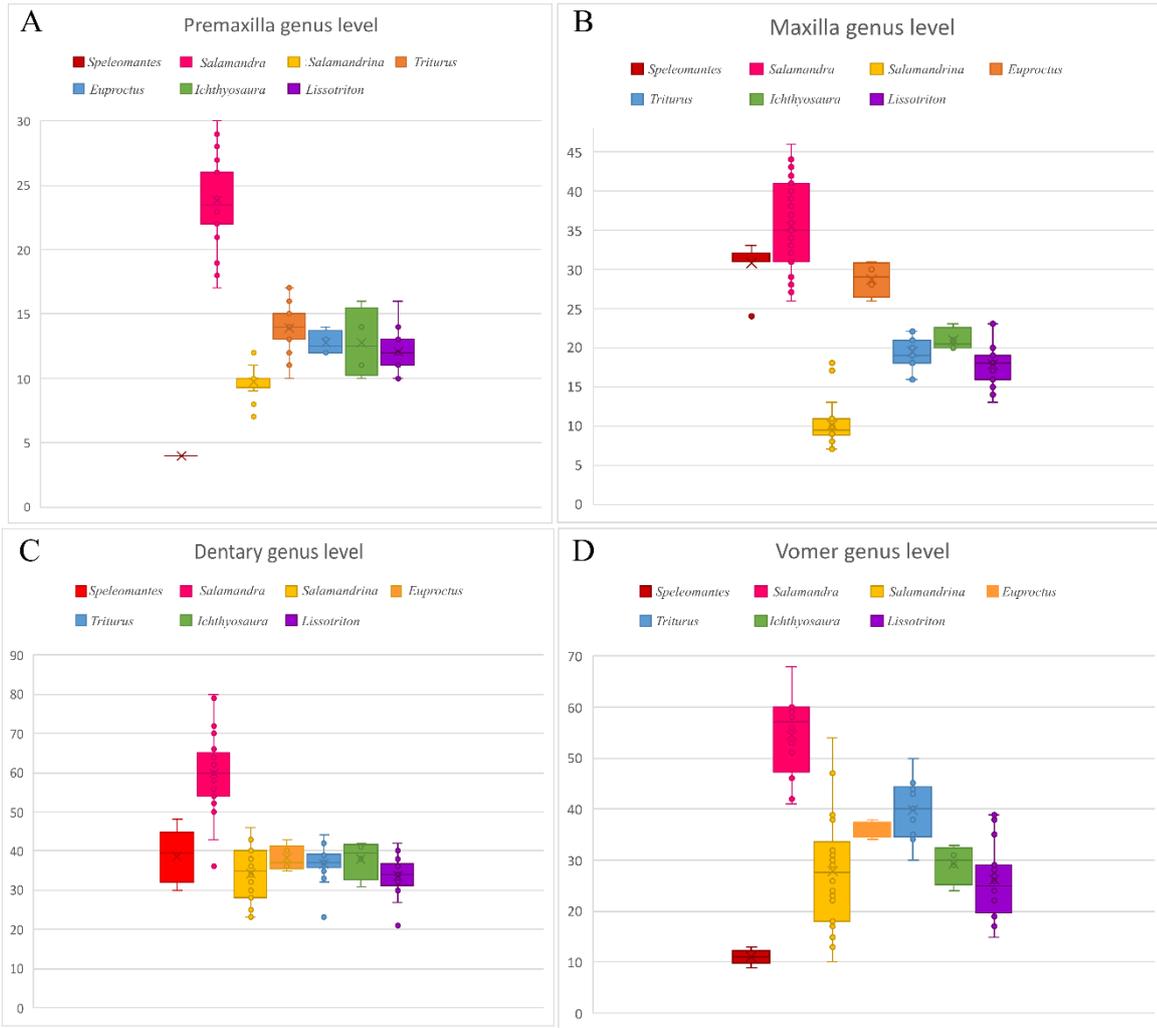
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