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

SARA MONTI, LOREDANA MACALUSO, MASSIMO DELFINO

Monti, S., Macaluso, L., Delfino, M. (2024): The tooth-bearing skeletal elements of the Italian urodeles, a comparative tool for osteological identification. Acta Herpetol. **19**. doi: 10.36253/a_h-15648.

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

SARA MONTI[1,*], LOREDANA MACALUSO[2], MASSIMO DELFINO[1,3]

[1] *Dipartimento di Scienze della Terra, Università di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy*

[2] *Sciences Collections, Martin Luther University Halle-Wittenberg, Domplatz 4, 06108 Halle (Saale), Germany*

[3] *Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Edifici ICTA-ICP, c/ Columnes, s/n, Campus de la UAB, E-08193 Cerdanyola del Vallès, Barcelona, Spain*

[*]*Corresponding author.* Email: sara.monti957@edu.unito.it

Submitted on: 2024, 31st January; revised on: 2024, 22nd March; accepted on: 2024, 8th May

Editor: Andrea Villa

Running title: Tooth-bearing elements of Italian urodeles

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

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

Keywords. Osteology, urodeles, phylogeny, dentigerous bones.

INTRODUCTION

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

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

MATERIAL AND METHODS

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

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

Comparative and phylogenetic analysis

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

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

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

RESULTS

Terminology and general morphology

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

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

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

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

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

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

Descriptions

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

Plethodontidae

Speleomantes

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

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

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

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

Salamandridae

Salamandrinae

Salamandra lanzai

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

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

Salamandra atra

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

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

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

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

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

Salamandra salamandra

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

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

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

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

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

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

Salamandrininae

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

Salamandrina

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

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

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

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

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

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

Pleurodelinae

Euproctus platycephalus

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

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

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

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

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

Triturus carnifex

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

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

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

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

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

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

Ichthyosaura alpestris

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

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

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

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

Lissotriton vulgaris

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

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

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

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

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

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

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

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

Comparative and phylogenetic analysis

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

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

DISCUSSION

Diagnostic characters

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

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

Speleomantes

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

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

671 (same in hynobiids). Pars facialis ending more posteriorly that 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 midlenght, 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.

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

Salamandrina

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

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

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

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

Subfamily Pleurodelinae

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

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

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

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

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

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

Premaxilla. Sculptured in anterior view.

Maxilla. Posterior sixth of pars dentalis toothless.

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

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

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

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

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

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.)

4. In posterior view, on the ventral half of the alary process, the medial margin can form two or three triangular expansions ……... *Salamandra salamandra*

- The alary process is thin, dorsally elongated and ends abruptly …….. 5

5. The pars palatina is extremely small and cannot be seen in anterior view …... *Salamandra lanzai*

- The pars palatina is poorly developed but can be seen in anterior view ……... *Salamandra atra**

6. In lateral view, the alary process shows an expansion that extends along its dorsal half, not visible in anterior and posterior views …….. *Speleomantes ambrosii**

- In anterior and posterior views, the alary process shows an expansion laterally directed that extends along its dorsal half …… *Speleomantes strinatii**

7. The dorsal portions of the alary processes remain close to each other along all their length …….. *Euproctus platycephalus*

- The dorsal portions of the alary processes point dorsolaterally, getting far from each other …….. 8

8. Ventral half of the alary process sculptured, with irregular pits and ridges …….. *Triturus carnifex*

- Ventral half of the alary process smooth or with a few foramina or cavities …….. 9

9. Anterior margin of the pars dentalis smooth and regular in posterior view and rather trapezoidal in shape ……. *Ichthyosaura alpestris*

- Anterior margin of the pars dentalis irregular in posterior view and rather semicircular in shape ……... 10 (*Lissotriton* spp.)

10. Left (or right) half of the premaxilla twice higher than long …….. *Lissotriton vulgaris*

- Premaxilla is as long as or slightly shorter than high …….. *Lissotriton italicus*

<u>Maxilla</u>

1. The posterior end of the pars dentalis is dorsally curved ……... *Salamandrina* spp.

- The pars dentalis is straight …….. 2

2. The teeth run for the whole length of the pars dentalis, including the processus maxillaris anterior. As such, the pars facialis does not reach the anterior end of the tooth row …….. *Speleomantes* spp.

- The pars facialis does not significantly extend on the processus maxillaris anterior, but it ends together with the tooth row anteriorly or the pars facialis extends more anteriorly than the tooth row, on the processus maxillaris anterior ……... 3

3. The pars facialis does not significantly extend on the processus maxillaris anterior, but it ends together with the tooth row anteriorly ……. 4 (*Salamandra* spp.)

- The pars facialis extends more anteriorly than the tooth row, on the processus maxillaris anterior ……. 6

4. The posterior fifth of the length of the pars dentalis is toothless …… *Salamandra atra**

- The posterior fourth of the length of the pars dentalis is toothless …….. 5

5. The pars facialis extends along the anterior third of the pars dentalis ….. *Salamandra salamandra*

- The pars facialis extends along the anterior half of the pars dentalis …….. *Salamandra lanzai*

6. The pars palatina keeps the same width for the anterior half of the pars dentalis; it narrows at the anterior end, partly participating to the sharp processus maxillaris anterior, with regular margins …… *Triturus carnifex*

- The pars palatina has the same width for almost its entire length; it either ends anteriorly in a flat, abrupt processus maxillaris anterior, with regular margins, or the pars palatina is subtriangular in shape, enlarging posterolaterally, or it has the same width for all his length except a widening at midlenght …… 7

7. No sculpturing on the pars facialis …… 8

- Pars facialis sculptured in lateral view, with irregular pits and ridges …… 9

8. Pars facialis extended for more than half of the pars dentalis …….. *Ichthyosaura alpestris*

- Pars facialis extended for half of the pars dentalis or less …….. *Lissotriton vulgaris*

9. Processus maxillaris anterior formed just by the pars facialis …….. *Euproctus platycephalus*

- Processus maxillaris anterior formed by the pars palatina and the pars facialis .. *Lissotriton italicus*

<u>Vomer</u>

1. In dorsal view, body of the vomer hammer shaped (see description above) …. *Salamandrina* spp.

826 - In dorsal view, body of the vomer triangular ……... 2

827 2. Processus vomeropalatinus minor is pointed and slender …… *Salamandra salamandra*

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 …… *Salamandra* 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° …….. *Speleomantes* 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 ……. *Euproctus platycephalus*

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 …….. *Ichthyosaura alpestris*

842 7. Processus vomeropalatinus minor rounded …… *Lissotriton italicus*

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 ……... *Triturus carnifex*

846 - Processus vomeropalatinus major short, giving the body of the vomer a rectangular shape

847 …… *Lissotriton vulgaris*

848 <u>Dentary</u>

849 1. The symphysis shows a dorsal bulge in medial view ……. *Speleomantes* spp.

850 - The symphysis is semicircular ……. 2

851 2. Dorsal and ventral margins fused for at least the anterior five sixths …… *Salamandrina* spp.

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

Variation in the number of tooth positions

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

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

Phylogenetic analysis

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

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

CONCLUSION

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

ACKNOWLEDGMENTS

This work is supported by Fondi di Ricerca Locale dell'Università degli Studi di Torino 2020-2022. LM received fundings from the Alexander von Humboldt Foundation (Humboldt Research Fellowship). SM received help from Dr. Marco Pavia in the form of providing access to the collection and technical support. Andrea Villa, Hugues-Alexandre Blain, and an anonymous reviewer are thanked for the useful comments on a previous version of the manuscript. This is the publication number XXX of the Museo di Geologia e Paleontologia collections at the Università degli Studi di Torino.

SUPPLEMENTARY MATERIAL

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

REFERENCES

Abbazzi, A., Angelone, C., Arca, M., Barisone, G., Bedetti, C., Delfino, M., Kotsakis, T., Marcolini, F., Palombo, M. R., Pavia, M., Piras, P., Rook, L., Torre, D., Tuveri, C., Valli, A. M. F., Wilkens, B. (2004): Plio-Pleistocene fossil vertebrates of Monte Tuttavista (Orosei, Eastern Sardinia, Italy), an overview. Riv. Itali. Paleontol. Stratigr. **110**: 681-706.

Buckley, D., Wake, M. H., Wake, D. B. (2010): Comparative skull osteology of *Karsenia koreana* (amphibia, caudata, plethodontidae). J. Morphol. **271**: 533-583.

Colombero, S., Alba, D., D'Amico, C., Delfino, M., Esu, D., Giuntelli, P., Harzhauser, M., Mazza, P.A.P., Mosca, M., Neubauer, T., Pavia, G., Pavia, M., Villa, A., Carnevale, G. (2017): Late Messinian mollusks and vertebrates from Moncucco Torinese, north-western Italy. Paleoecological and paleoclimatological implications. Palaeontol. Electron. **20**: 1-66.

Deban, S.M., Wake, D.B. (2000): Aquatic feeding in salamanders. In: Feeding: form, function and evolution in tetrapod vertebrates, pp. 65-94. Schwenk, K., Ed., Academic Press, San Diego.

Delfino, M. (2004): The Middle Pleistocene herpetofauna of Valdemino Cave (Liguria, North-Western Italy). Herpetol. J. **14**: 113-128.

Delfino, M., Bailon, S. (2000): Early Pleistocene herpetofauna from Cava Dell'Erba and Cava Pirro (Apulia, Southern Italy). Herpetol J. **10**: 95-110.

Delfino, M., Pitruzzella, G., Bailon, S. (2011): The Late Pliocene amphibians and reptiles from "Capo Mannu D1 Local Fauna" (Mandriola, Sardinia, Italy). Geodiversitas **33**: 357-382.

D'Orazi Porchetti, S., Sottili, G. (2012): A salamandrid from the middle Pleistocene of northern Latium (Fosso di San Martino, Rome, Italy). Boll. Soc. Paleontol. Ital. **51**: 7-13.

Duellman, W., Trueb, L. (1994): Biology of amphibians. Johns Hopkins University Press, Baltimore.

Fabre, A.C., Bardua, C., Bon, M., Clavel, J., Felice, R.N., Streicher, J.W., Bonnel, J., Stanley, E.L., Blackburn, D.C., Goswami, A. (2020): Metamorphosis shapes cranial diversity and rate of evolution in salamanders. Nat. Ecol. Evol. **4**: 1129-1140.

Goloboff, P., Morales, M. (2023): TNT version 1.6, with a graphical interface of MacOs and Linux, iincluding new routines in parallel. Cladistics **39**: 144-153.

Jia, J., Gao, K., Jiang, J., Bever, G., Xiong, R., Wei, G. (2021): Comparative osteology of the hynobiid complex *Liua-Protohynobius-Pseudohynobius* (Amphibia, Urodela): I. Cranial anatomy of *Pseudohynobius*. J. Anat. **238**: 219-248.

Kohno, S., Kuro-o, M., Ikebe, C. (1991): Cytogenetics and evolution of hynobiid salamanders. In: Amphibian cytogenetics and evolution, pp. 67-88. Green D.M., Sessions, S.K., Eds, Academic Press, San Diego.

Lanza, B., Corti, C. (1996): Evolution of the knowledge on the Italian herpetofauna during the 20th century. Boll. Museo St. Nat. Verona **20**: 373-436.

Lanza, B., Andreone, F., Bologna, M.A., Corti, C., Razzetti, E. (2007): Amphibia. Fauna d'Italia. Edizioni Calderini de Il Sole 24 Ore, Bologna.

Macaluso, L., Villa, A., Pitruzzella, G., Rook, L., Carnevale, G., Delfino, M. (2021a): A progressive extirpation: an overview of the fossil record of *Salamandrina* (Salamandridae, Urodela). Hist. Biol. **33**: 3723-3740.

Macaluso, L., Villa, A., Carnevale, G., Delfino, M. (2021b): Past, present, and future climate space of the only endemic vertebrate genus of the Italian peninsula. Sci. Rep. **11**: 22139.

Macaluso, L., Mannion, P., Evans, S., Carnevale G., Monti, S., Marchitelli, D., Delfino, M. (2022): Biogeographic history of Palearctic caudates revealed by a critical appraisal of their fossil record quality and spatio-temporal distribution. R. Soc. Open Sci. **9**: 220935.

Macaluso, L., Bertini, A., Carnevale, G., Eronen, J. T., Martinetto, E., Saarinen, J., Capasso, F., Delfino, M. (2023a): A combined palaeomodelling approach reveals the selective role as

refugia of the Mediterranean peninsulas. Palaeogeogr. Palaeoclimatol. Palaeoecol. **625**: 111699.

Macaluso, L., Wencker, L., Castrovilli, M., Carnevale, G., Delfino, M. (2023b): A comparative atlas of selected skeletal elements of European urodeles (Amphibia: Urodela) for palaentological investigations. Zool. J. Linn. Soc. **197**: 569-619.

Maddison, W., Maddison D. R. (2019): Mesquite: a modular system for evolutionary analysis. Version 3.61.

Marjanovic, D., Witzmann, F. (2015): An extremely peramorphic newt (Urodela: Salamandridae: Pleurodelini) from the latest Oligocene of Germany, and a new phylogenetic analysis of extant and extinct salamandrids. PLoS ONE. **10**: e01370688.

Monti, S. (2021): Il record fossile e le origini dell'attuale diversità dei caudati paleartici. Bachelor's thesis, Università degli Studi di Torino.

Pyron, R., Wiens, J. (2011): A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. Mol. Phylogenet. Evol. **61**: 543-583.

Ratnikov, V., Litvinchuk, S. (2007): Comparative morphology of trunk and sacral vertebrae of tailed amphibians of Russia and adjacent countries. Russ. J. Herpetol. **14**: 177-190.

Ratnikov, V., Litvinchuk, S. (2009): Atlantal vertebrae of tailed amphibians of Russia and adjacent countries. Russ. J. Herpetol. **16**: 57-68.

Ratnikov, V. (2015): Comparative humeral morphology of some Eurasian tailed amphibians (Amphibia, Urodela) for palaeontological studies. Acta Zool. Cracov. **58**: 101-119.

Rancilhac, L., Irisarri, I., Angelini, C., Arntzen, J. W., Babik, W., Bossuyt, F., Kunzel, S., Luddecke, T., Pasmans, F., Sanchez, E., Weisrock, D., Veith, M., Wielstra, B., Steinfartz, S., Hofreiter, M., Philippe, H., Vences, M. (2021): Phylotranscriptomic evidence for pervasive ancient hybridization among Old World salamanders. Mol. Phylogenet. Evol. **155**: 106967.

1031 Schoch, R.R. (2014): Amphibian Evolution: The Life of Early Land Vertebrates. Wiley-Blackwell,
1032 Hoboken.
1033 Vater, M. (2003): Anatómia kostrovej sústavy mloka vrchovského (*Triturus alpestris*) a jej
1034 ontogenéza (Vol. 132). PhD thesis, Praha: Přírodovědecká Faculta University Karlovi.
1035 Venczel, M., & Sanchiz, B. (2006): Lower Miocene Amphibians and Reptiles from Oschiri (Sardinia,
1036 Italy). Hantkeniana **5**: 72-75.
1037 Villa, A., Andreone, F., Boistel, R., Delfino, M. (2014): Skull and lower jaw osteology of the Lanza's
1038 salamander, *Salamandra lanzai* (Amphibia, Caudata). In: Scripta Herpetologica. Studies on
1039 amphibians and reptiles in honour of Benedetto Lanza, pp. 171-200. Capula, M., Corti, C., Eds,
1040 Edizioni Belvedere, Latina.
1041 Villa, A., Blain, H., Delfino, M. (2018): The Early Pleistocene herpetofauna of Rivoli Veronese
1042 (Northern Italy) as evidence for humid and forested glacial phases in the Gelasian of Southern
1043 Alps. Palaeogeogr. Palaeoclimatol. Palaeoecol. **490**: 393-403.
1044 Villa, A., Bon, M., Delfino, M. (2020): Trapped in a roman well: Amphibians and reptiles from
1045 Tenuta Zuccarello near Marcon, Venice, Italy. Hist. Biol. **32**: 55-70.
1046 Villa, A., Carnevale, G., Pavia, M., Rook, L., Sami, M., Szyndlar, Z., Delfino, M. (2021): An
1047 overview on the late Miocene vertebrates from the fissure fillings of Monticino Quarry
1048 (Brisighella, Italy), with new data on non-mammalian taxa. Riv. Ital. Paleontol. Stratigr. **127**:
1049 297-354.
1050 Zhang, P., Papenfuss, T., Wake, M., Qu, L., Wake, D. (2008): Phylogeny and biogeography of the
1051 family Salamandridae (Amphibia: Caudata) inferred from complete mitochondrial genomes.
1052 Mol. Phylogenet. Evol. **49**: 586-597.
1053

1054 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 laeral (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*

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

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

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

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

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

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

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

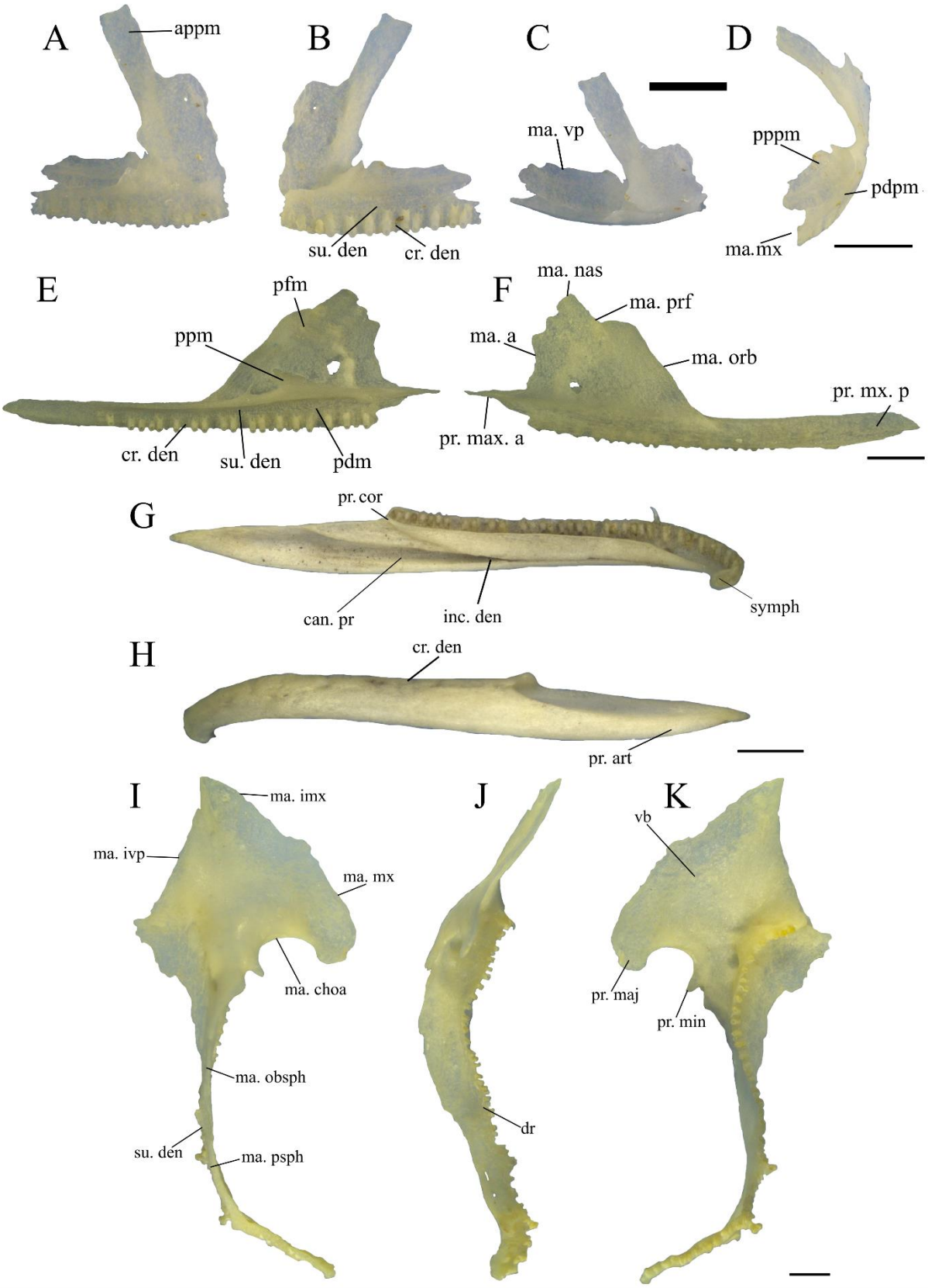
Fig. 8. Vomers of Italian urodeles. A-C: left vomer of *Speleomantes ambrosii* (MDHC 301) in dorsal (A), lateral (B) and medial (C) views; D-F: right vomer of *Speleomantes strinatii* (MDHC 486) in dorsal (D), lateral (E) and medial (F) views; G-I: left vomer of *Salamandra lanzai* (MDHC 362) in dorsal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

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

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

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

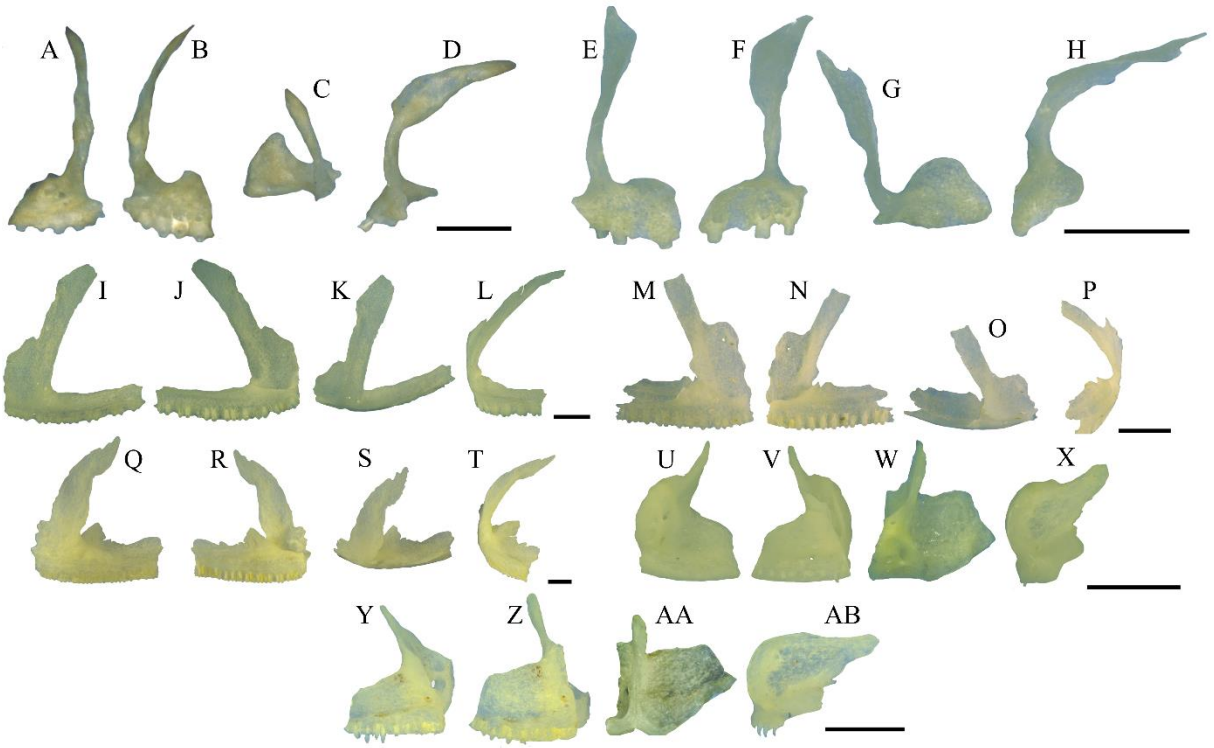
1146 Fig. 1



1147

1148

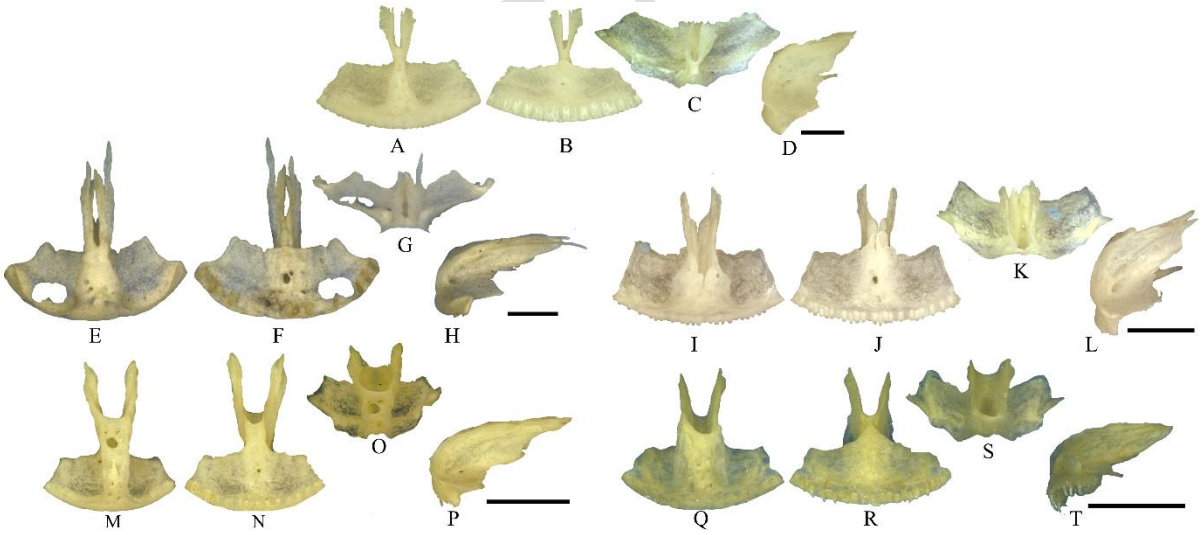
1149 Fig. 2



1150

1151

1152 Fig. 3



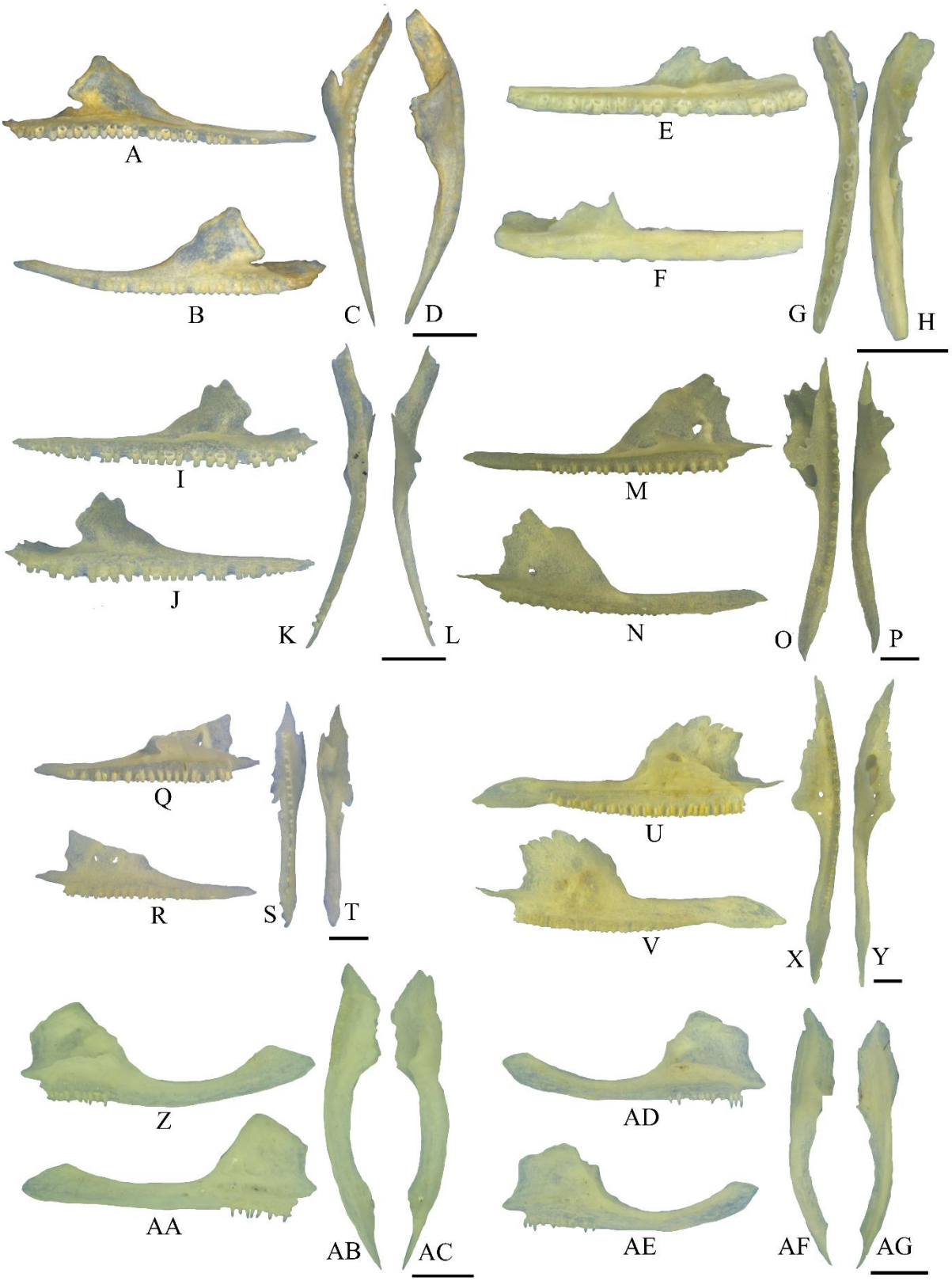
1153

1154

1155

1156

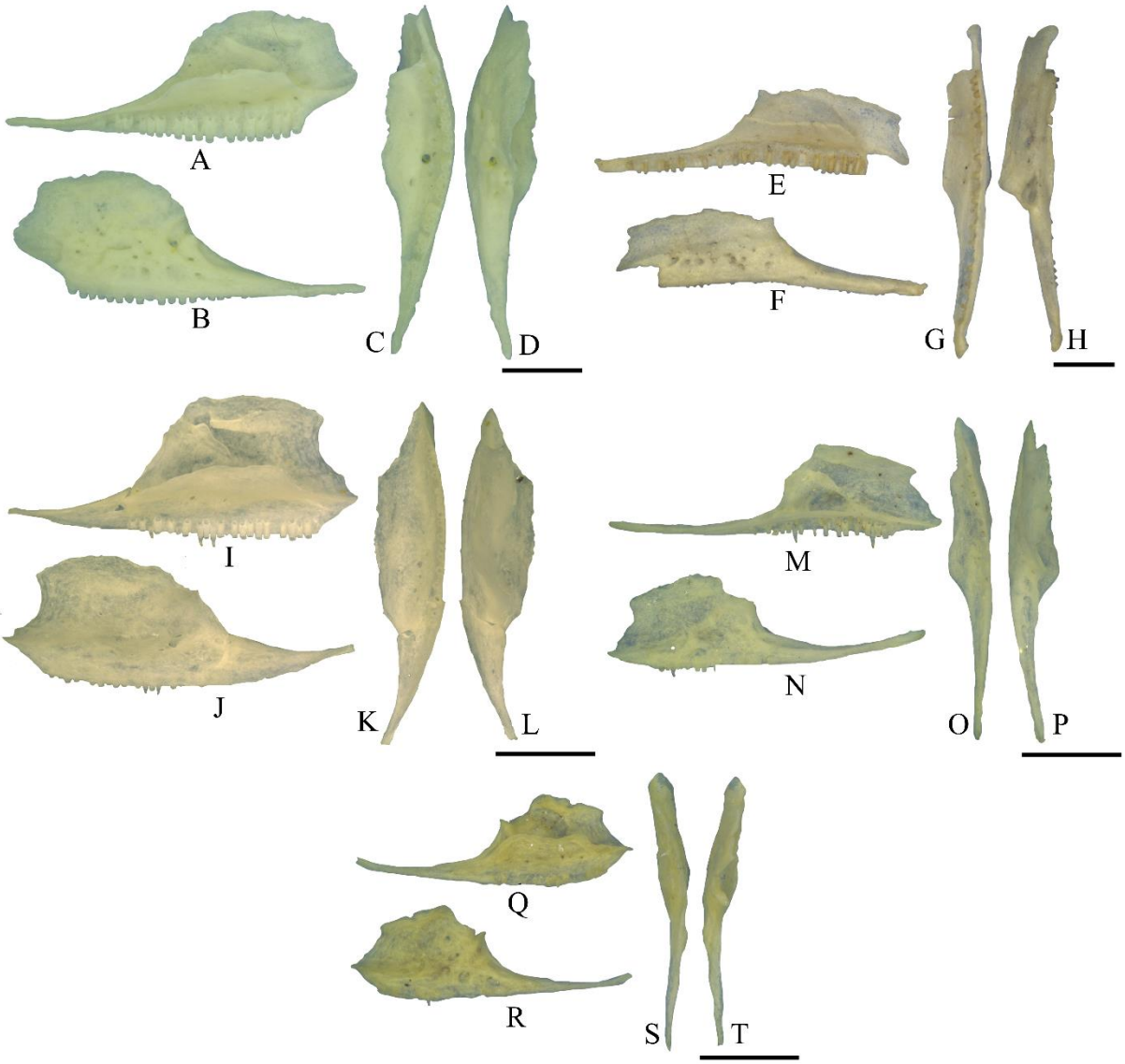
1157 Fig. 4



1158

1159

1160 Fig. 5

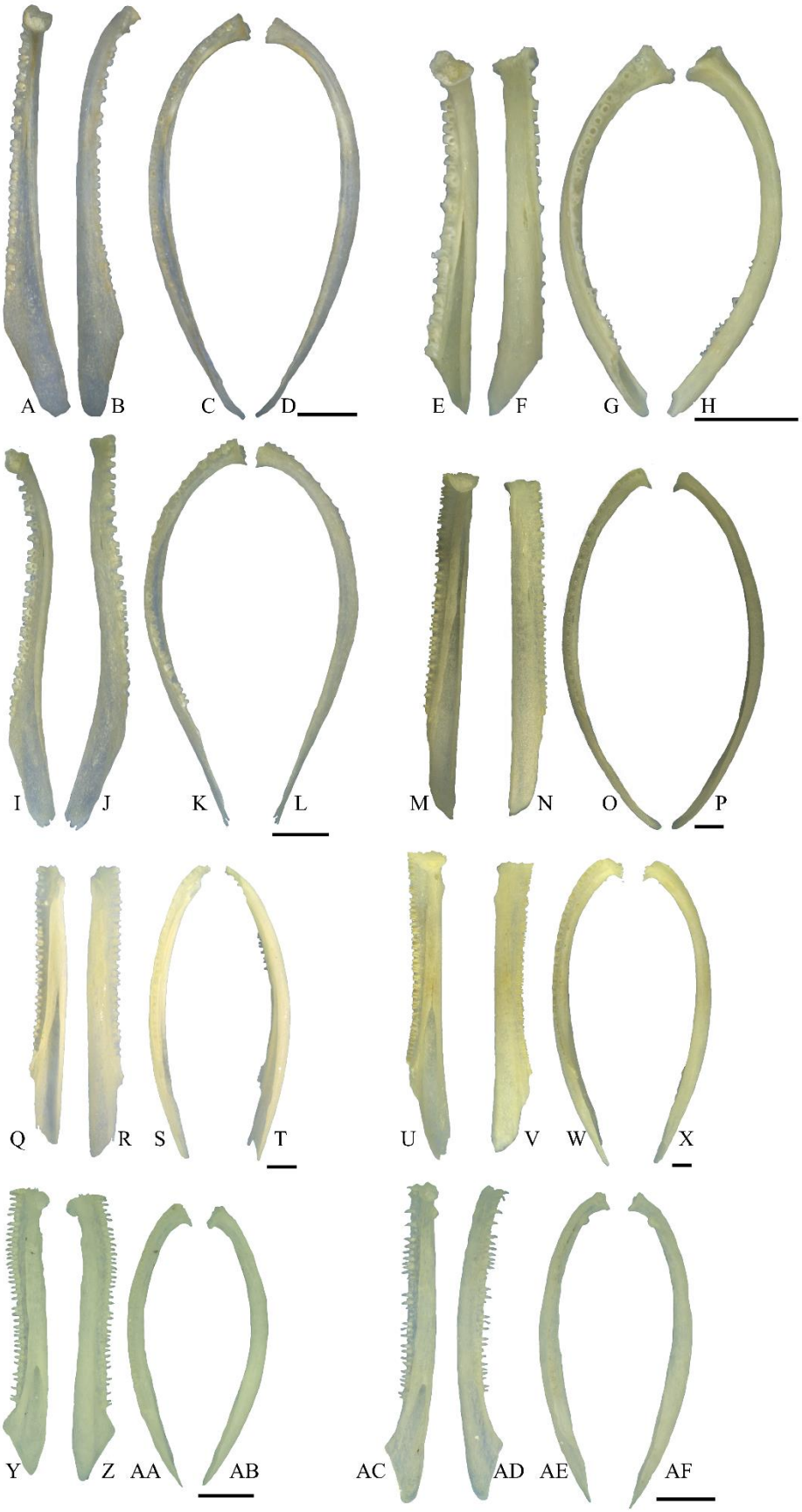


1161

1162

1163

1164 Fig. 6



1165

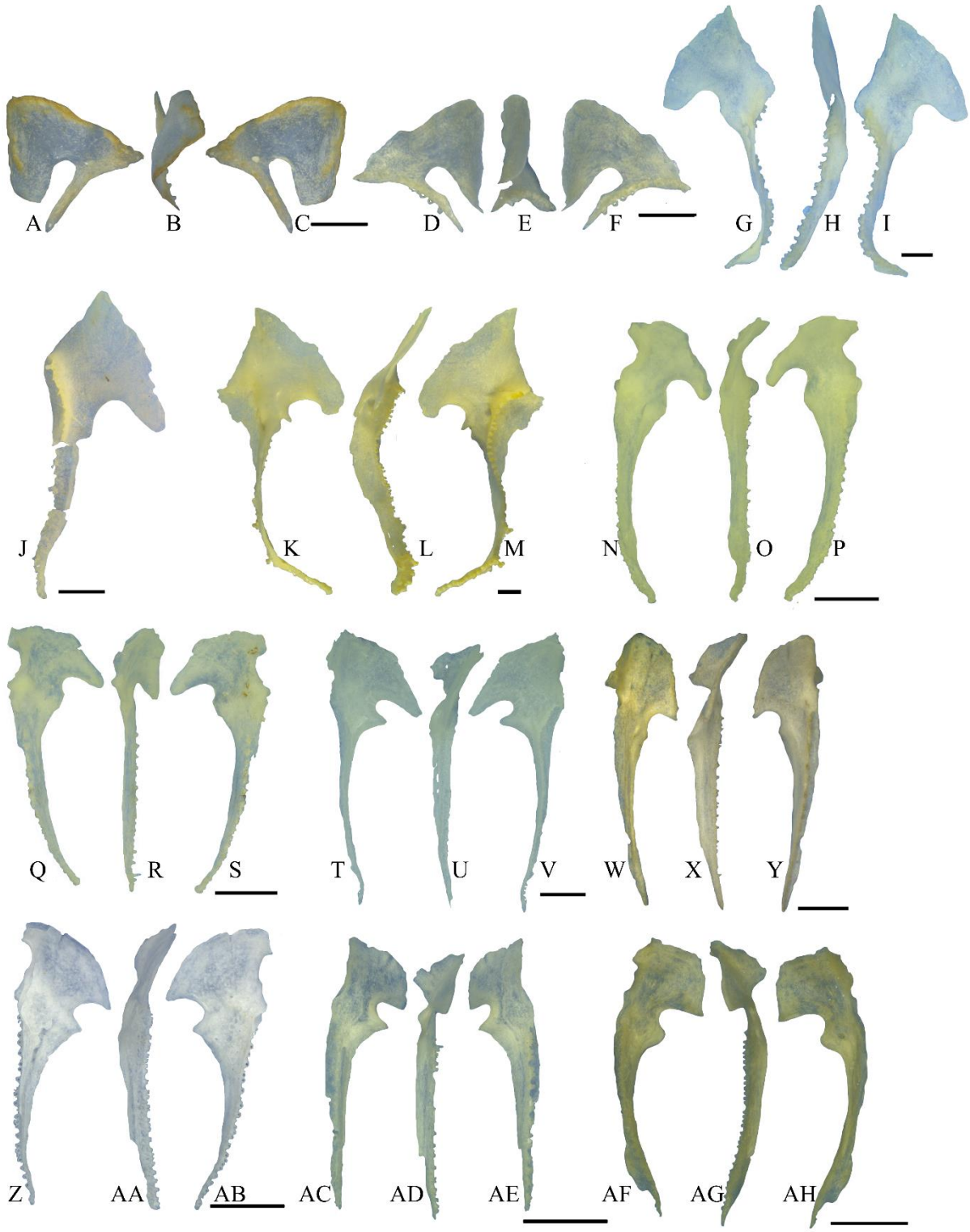
1166

1167 Fig. 7

1168

1169

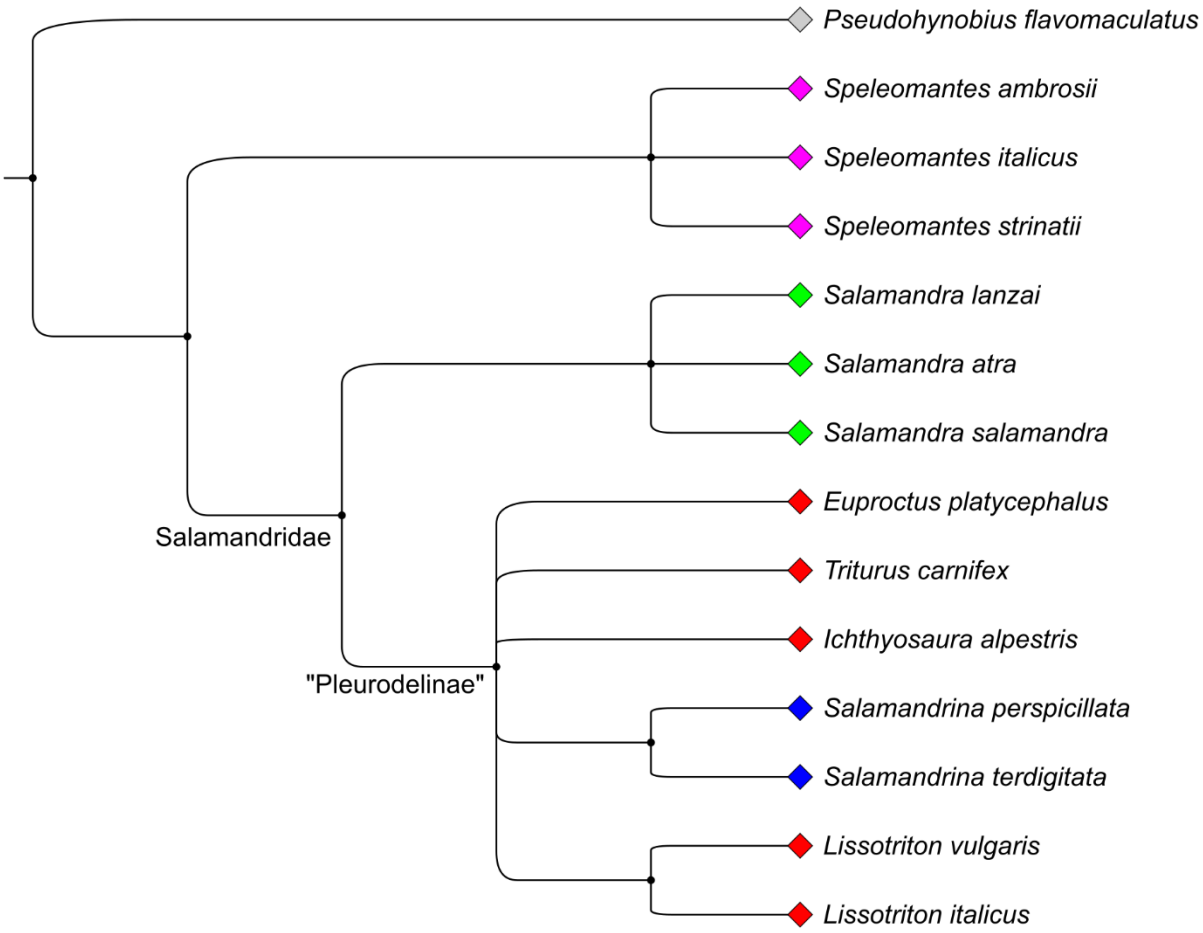
1170 Fig. 8



1171

1172

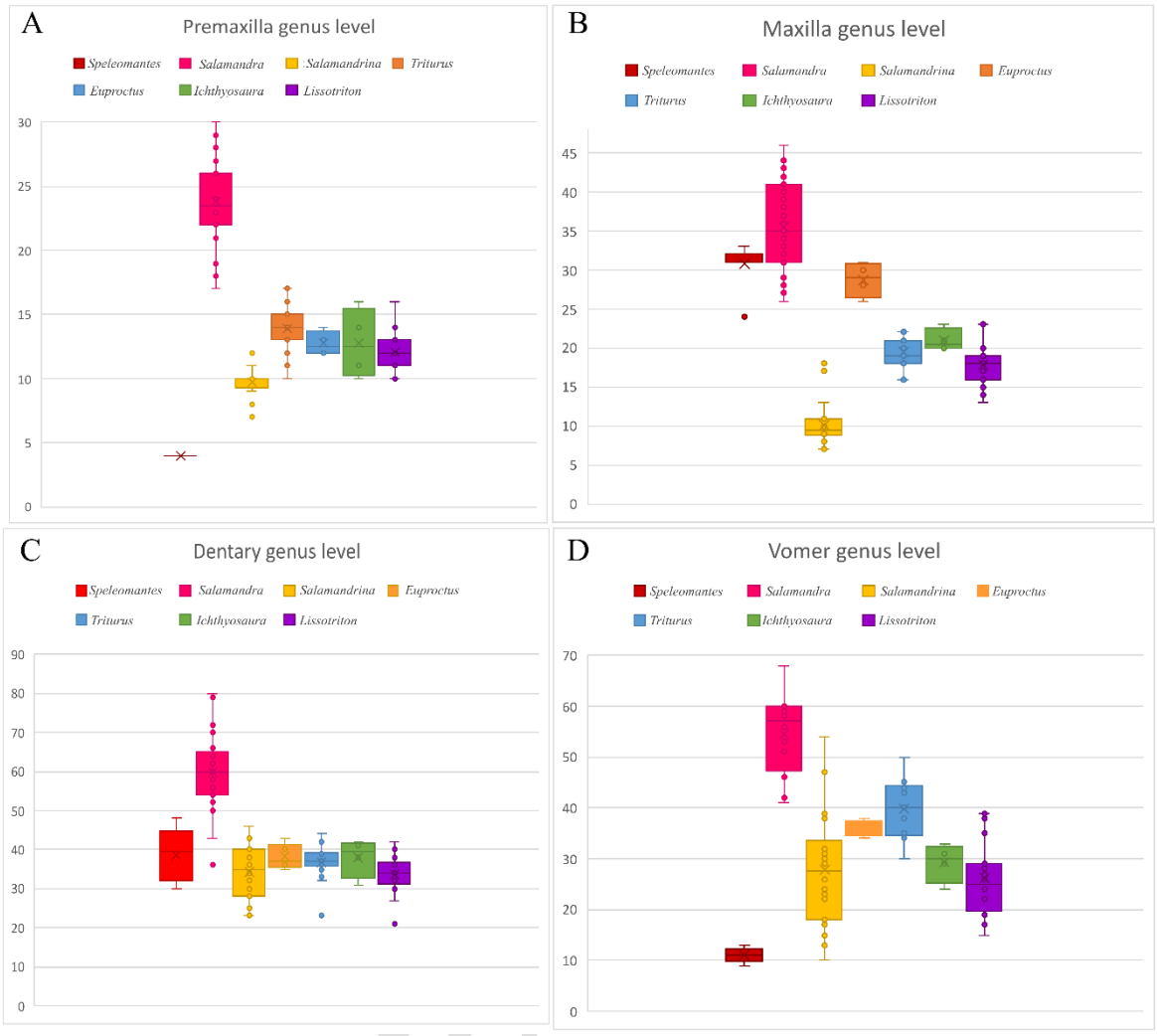
1173 Fig. 9



1174

1175

1176 Fig. 10



1177