# Cranial anatomy of *A. adriaticus* and extreme durophagous adaptations in Eusuchia (Reptilia: Crocodylomorpha)

Marco Muscioni[1, 2], Alfio Alessandro Chiarenza[3], Diego Bladimir Haro Fernandez[4, 5], Diego Dreossi[4], Flavio Bacchia[6], Federico Fanti[1, 2]

[1]Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Alma Mater Studiorum, Università di Bologna, via Zamboni 33, 40126 Bologna, Italy

[2]Museo Geologico Giovanni Capellini, Università di Bologna, via Zamboni 63, 40126 Bologna, Italy

[3]Department of Earth Sciences, University College London, Gower Pl, WC1E 6BS, London, UK

[4]SYRMEP Group, Elettra-Sincrotrone Trieste S.C.p.A. S.S. 14, km 163,5 in Area Science Park34149 Basovizza, Trieste, Italy

[5]Dipartimento di Fisica, Università della Calabria, Ponte Pietro Bucci, 31c, 87036 Quattromiglia, Italy

[6]Zoic Limited Liability Company, Trieste, Italy
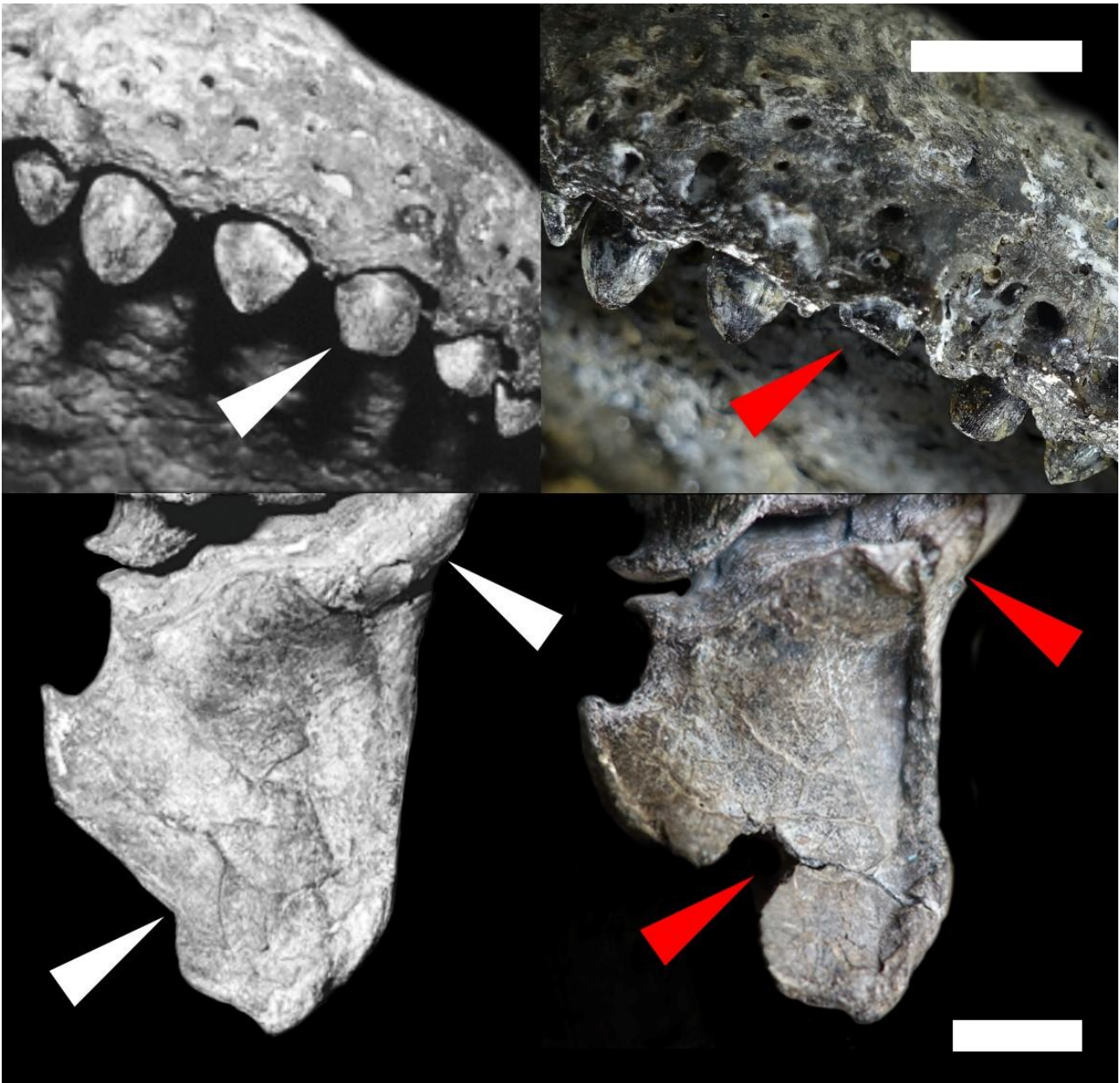
# SUPPLEMENTARY INFORMATION 1

**Figure S1.** Detail of the mechanical damage that occurred since the last formal inspection of the specimen MCSNT 57248. Pictures on the left are from Delfino et al. (2008a), pictures on the right were taken during this study. The arrows point to missing fragments before (white) and after (red), namely the 5th left premaxillary tooth (top) and portions of the right articular (bottom). Scale bar = 10 mm.

## Stratigraphic and ecologic context of *Acynodon adriaticus*

Overall, six lithofacies have been distinguished at the VdP site (see Tarlao et al., 1993, 1995; Attura, 1999; Palci, 2003; Arbulla et al., 2006; Dalla Vecchia, 2008, 2009; Cucchi & Piano, 2013; Chiarenza et al., 2021; Consorti et al., 2021; Muscioni et al., 2023), although their complex, reciprocal architecture remains barely documented. A new interpretation of facies distribution and associated benthic foraminifera biozones revised the age of the site to the latest early Campanian–earliest middle Campanian, a time interval of roughly 1 My, comprised between 81.5 and 80.5 Ma (see Chiarenza et al., 2021 for detailed discussion). However, a few remarks are necessary to properly support the paleoecological inferences for *Acynodon adriaticus* presented in this study.

Paleogeographic reconstructions suggesting that areas of the Adriatic Carbonatic Platform system (AdCP) constituted emerged islands during the Campanian have led to assumptions about insularity-driven evolutionary and biogeographical dynamics for the resident terrestrial biota (Dalla Vecchia, 2008, 2009, 2020). However, unequivocal data on the effective geographic extents and precise time indicators of the duration of spatial segregation of emerged areas remain largely undocumented. Mounting evidence points towards different scenarios for some latest Cretaceous megafaunas of the eastern Mediterranean region, with supposedly stereotypical insular traits (i.e., small size or taxonomically imbalanced communities) interpreted as retained plesiomorphic features and/or potentially explained by representative biases (Chiarenza et al., 2021; Nikolov et al., 2024).

During the early-middle Campanian, the VdP site would have been located at the northern edge of the tropical belt, with climate modelling of the Campanian suggesting warm conditions and possibly highly seasonal rainfall patterns, coherent with tropical savannah-like conditions (de Winter et al., 2021; Burgener et al., 2023). Geochemical and paleoenvironmental data from the VdP fossil beds indicate conditions ranging from brackish to lacustrine with acidic pH, frequent anoxia, and potentially marked seasonality (Arbulla et al., 2000; Palci, 2003; Arbulla et al., 2006). New geochemical data (Baldassarri, 2024) indicate that the fossiliferous rhythmites were deposited in a marginal context not compatible with either marine or inland bodies of water, characterized by high biological productivity, varying degrees of terrigenous sediment supply, and recurrent anoxic to dysoxic conditions. Similarly, available data on forams and algal communities support slightly brackish to freshwater conditions (Palci, 2003). The occurrence of a relatively diverse arthropod fauna comprising crustaceans and insects, along with revised macrofloral remains, may also suggest a less marine-influenced environment (Muscioni et al., 2024; Muscioni et al., in prep.). A complete palynological and macrofloral re-evaluation is currently ongoing, and available evidence may support a rich plant community.

The taphonomy of the site remains problematic; small vertebrates and invertebrates are mostly disarticulated, whereas remains of larger vertebrates are often articulated and show potential evidence of temporary subaerial exposure and desiccation (e.g., flaky, brittle bone surfaces, arched articulated vertebral series, complete shifted osteoderm shield on MCSNT 57031). *A. adriaticus* specimens described in this paper were found within the same highly productive interval made of a single, syn-depositional, slumped set of rhythmites, together with the holotype of the hadrosauroid *Tethyshadros insularis* (Chiarenza et al., 2021), other disarticulated *A. adriaticus* elements (see Muscioni et al., 2023), undetermined crocodylomorph and pterosaur material (Dalla Vecchia, 2017), as well as undescribed teleost fishes, arthropods, molluscs, and megafloral remains.

**Diagenetic deformation of the holotype**

The skull is dorsoventrally compressed so that the cranial roof and the dorsal surface of the maxillae and jugals are on the same horizontal level. At the same time, a fracture is visible on the dorsal surface of the anterior region, extending from the posterior area of the external naris to the orbits, running parallel to the labial margin of the skull. The dorsal surface of the nasal and maxillae between the two fractures is positioned at a lower level than the lateral, labial margins of the skull. Tomographic sections demonstrate how the less deformed external margin of the fracture coincides with the anterior teeth alveoli. Considering the substantial continuity in the dorsoventral volume down to the posterior labial margins of the maxillae, we conclude that the in-place dentition itself added considerable mechanical resistance against compression. This resulted in differential deformation, with the medial areas of the skull subject to more severe flattening.

Maxillary molariforms are not oriented perpendicularly to the mediolateral axis of the skull but are inclined obliquely with the crowns facing slightly lingually. Although it is possible that this condition represents the original anatomy of the skull, it is more likely a diagenetic artifact. The re-orientation of the external margins of the maxilla could have been produced by a "curling" against the margins of the mandible, and a lateral expansion of the posterior portion of the skull. This morphology was produced by the downward push of the plastically compressed cranial roof, which does not show any evident fracture from the surrounding elements. According to this interpretation, the original morphology of the skull of MCSNT 57248 would preserve the general dorsoventrally flattened and mediolaterally expanded shape observable from the fossil; however, the dorsal portion of the rostrum and the entire cranial roof would have originally been located slightly above their current position.

This would imply a consequent slight mediolateral narrowing of the posterior portion of the skull and partial re-orientation of the upper molariforms.

The mandible of MCSNT 57248, except for a probable slight lingual rotation of the lower margin of the mandibular rami due to the dorsoventral compression, appears to have undergone little to no deformation from the retroarticular processes up to the mid-extension of the dentaries. The retroarticular processes themselves extend posteriorly; their dorsal surface lies subhorizontally while their ventral portion describes a gentle dorsal inclination. The anterior half of the mandible is visibly compressed. The symphyseal area is naturally flattened in shape but may have been affected by a slight horizontal re-orientation starting from a more oblique condition. The segmented dentition seems to show clear signs of compression and slight horizontal re-orientation. In agreement with the already mentioned rotation of the mandibular rami on their axis, the hemimandible portions immediately posterior to the symphysis appear to be placed horizontally, with the ventral surface representing the original lateroventral surface. Retrodeformation of the skull should therefore produce a morphology that is generally less dorsoventrally compressed, slightly less mediolaterally expanded, and with the posterior portions of the jugal and maxilla oriented less horizontally.

**Figure S2. Representation of the dorsoventral compression of the rostral preorbital area (a) and temporal area (b) through tomographic slices. Schematic quantification of original (pre) and deformed (post) shape on the relative CT sections are represented inside the white boxes on the right. The red lines on the bottom left miniatures represents the relative slice location on the x-ray pictures of the skull. Maxillary teeth are highlighted in purple, dentary teeth in light blue.**
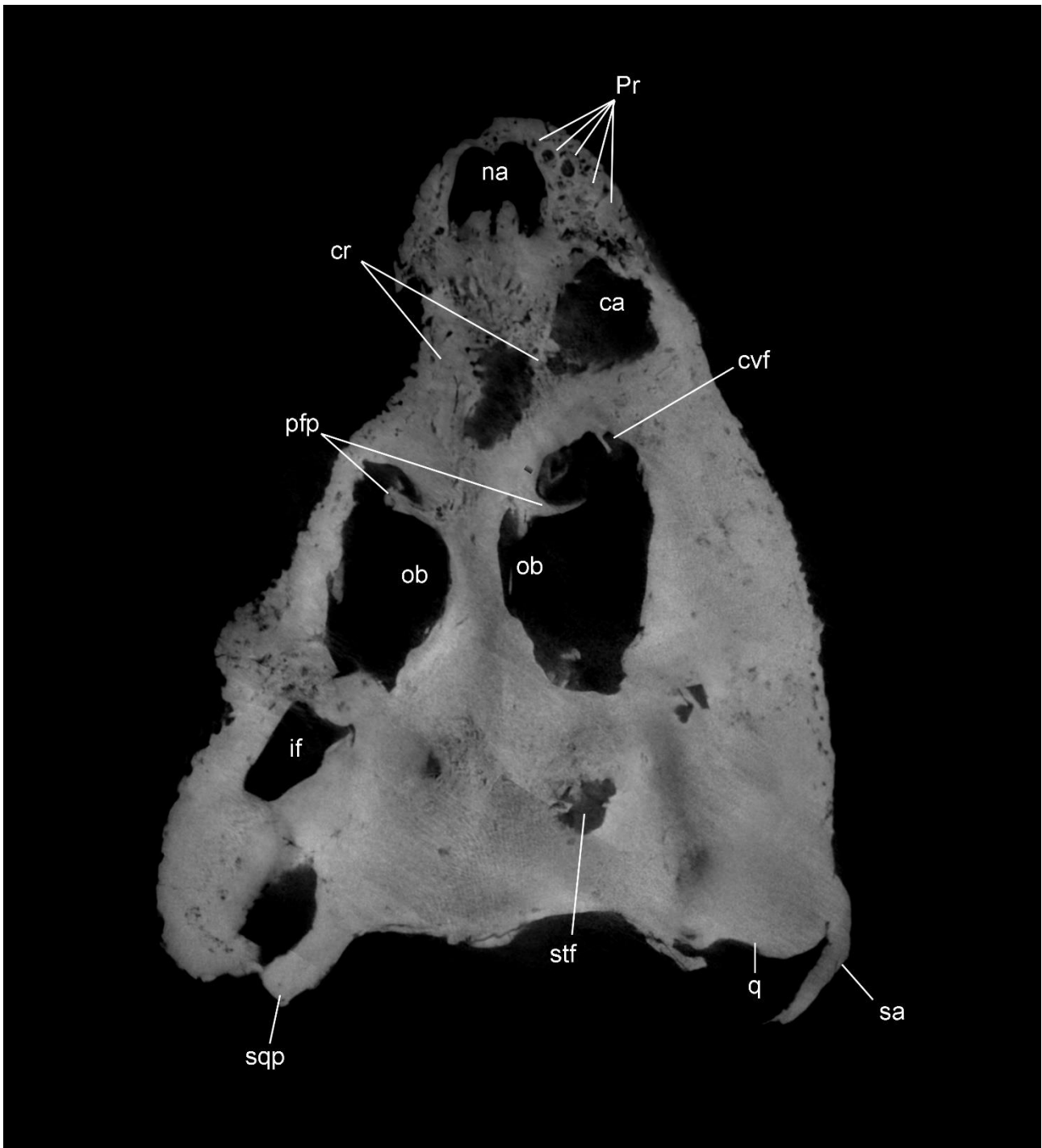
(a)

post

pre

(b)

post

pre
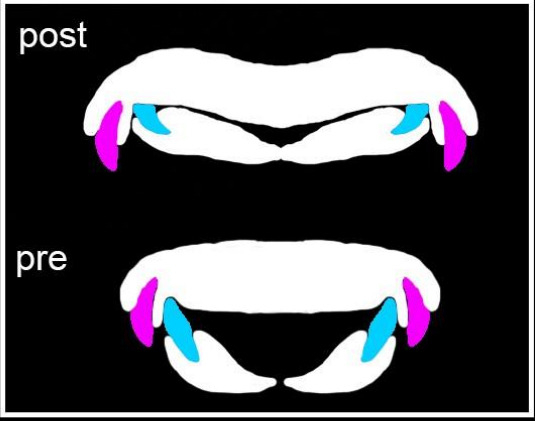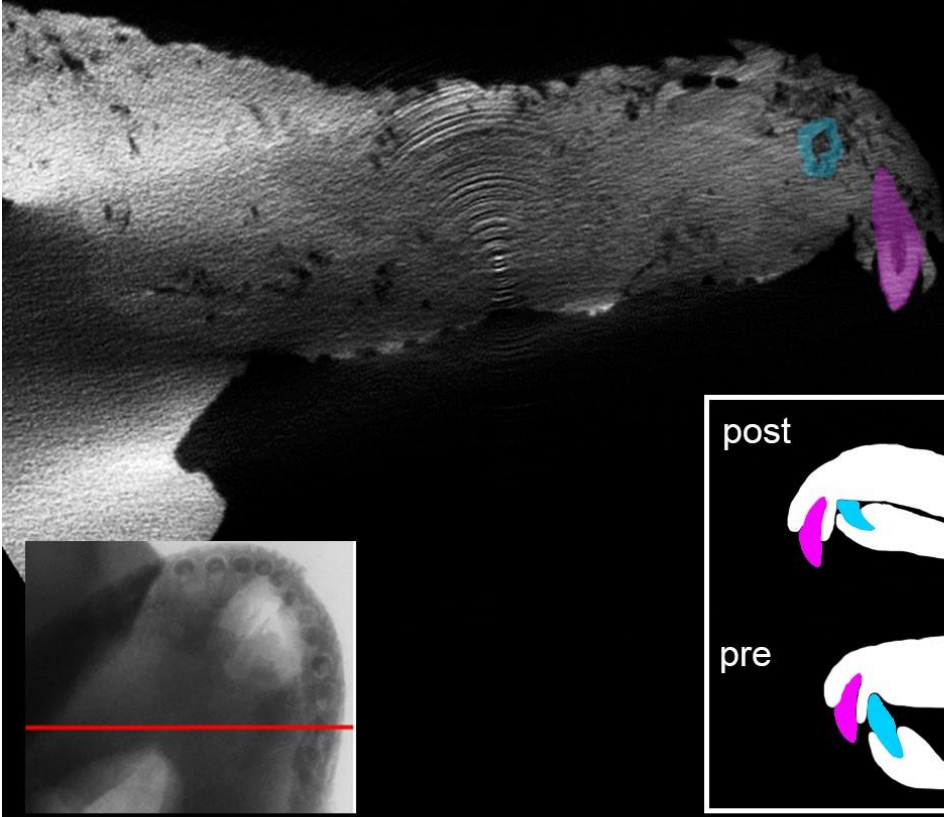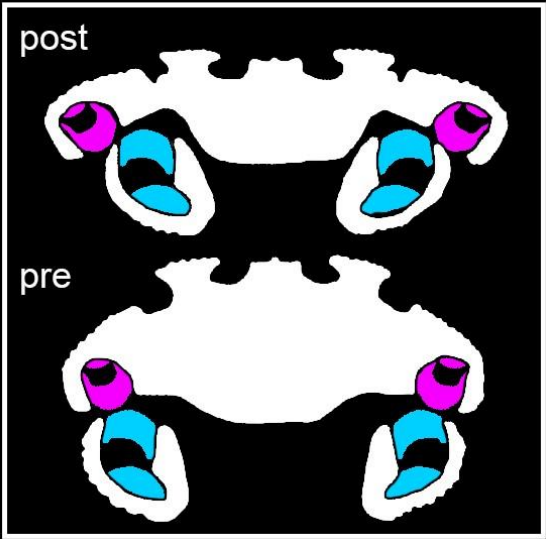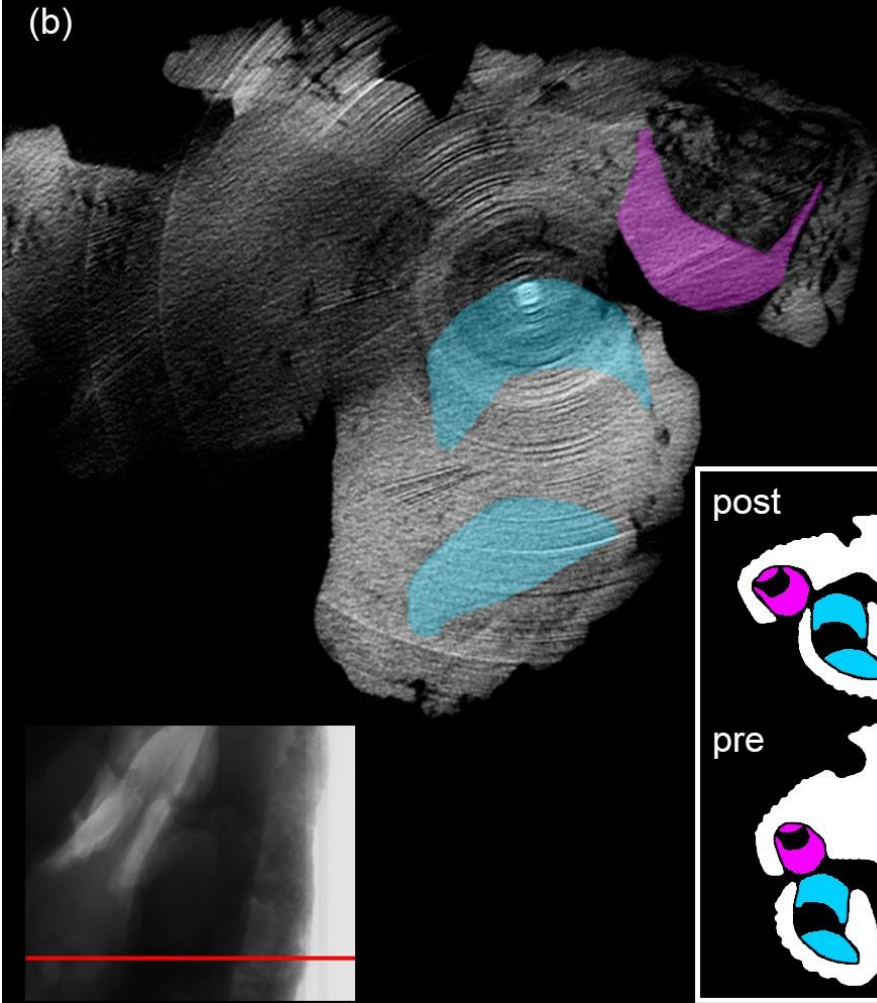
**Figure S3. Horizontal slice of MCSNT 57248. ca = collapsed area, cr = "canthi rostralii", cvf = caviconchal fossa, if = infratemporal fenestra, na = naris, ob = orbit, pfp = prefrontal pillar, Pr = premaxillary roots, q = quadrate, sa = surangular., sqp = squamosal prong, stf = supratemporal fenestra.**
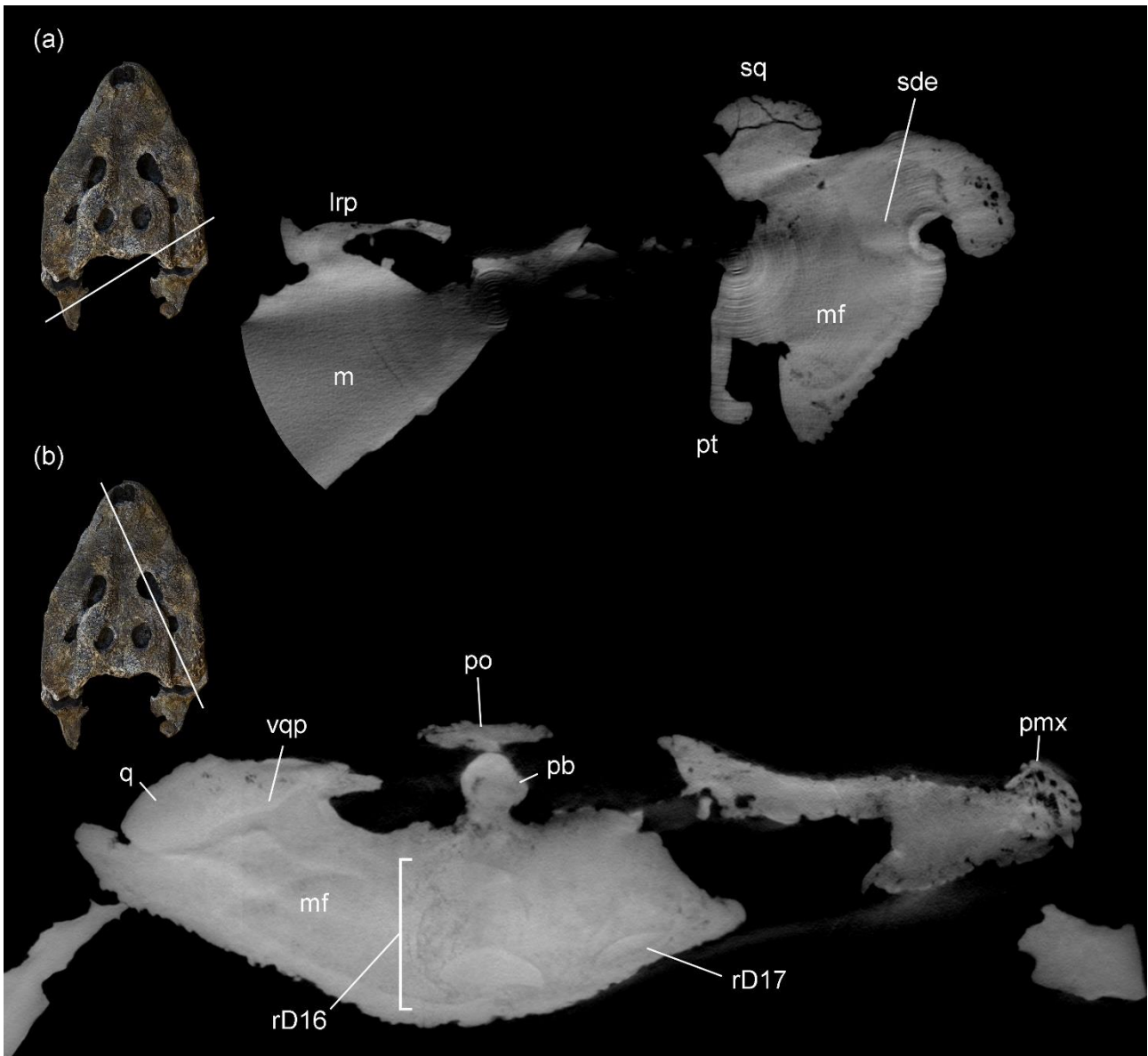
**Figure S4. Vertical slices of MCSNT 57248. Note the articulated replacement molariform teeth in (b). lrp = left retroarticular process, m = matrix, mf = mandibular fossa, pb = postorbital bar, pmx = premaxilla, po = postorbital, pt = pterygoid, q = quadrate, rD = right dentary tooth, sde = surangular dorsal expansion, sq = squamosal, vqp = ventral quadrate protuberance.**
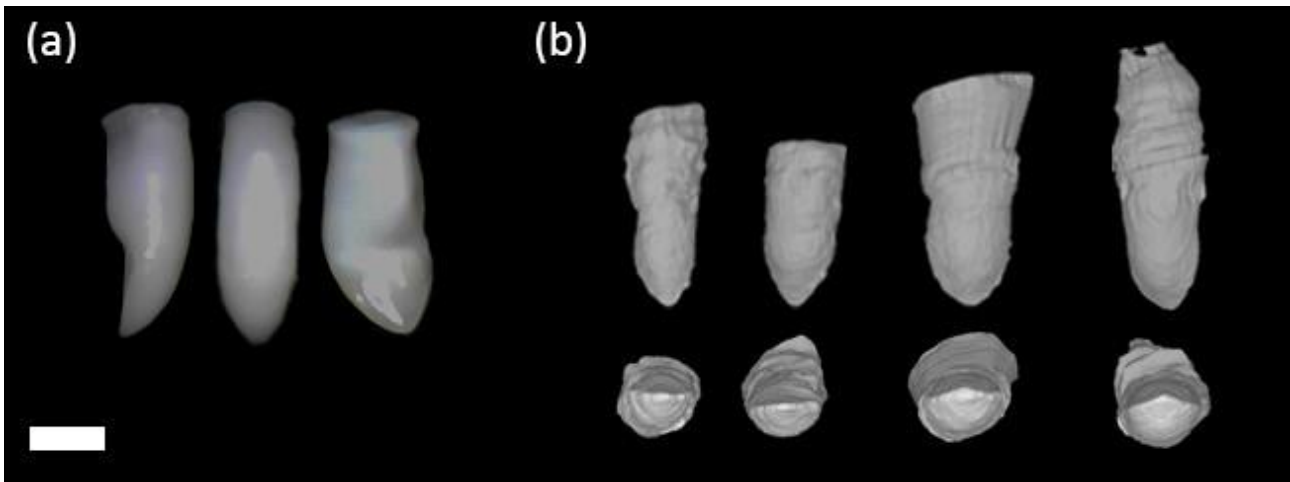
**Figure S5.** Comparison between three different incisiviform teeth of the durophagous sparid *Sparus aurata* from different views (a) and surface rendering of the left premaxillary teeth 1-4 of *Acynodon adriaticus* in labial (top) and occlusal (bottom) view. Scale bar = 1 mm refers to the *Sparus* teeth; *A. adriaticus* teeth not for scale.
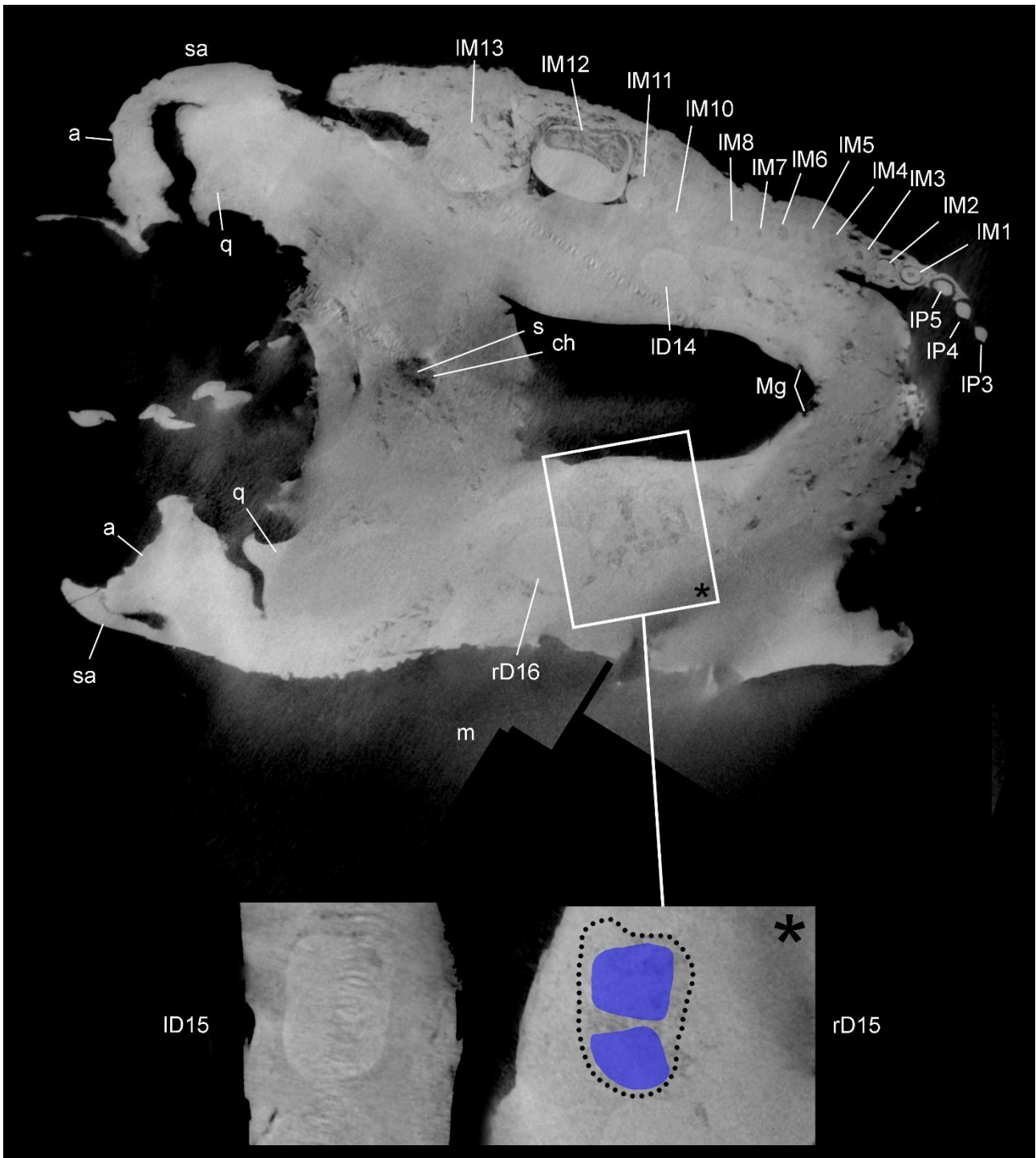
**Figure S6. Horizontal slice of MCSNT 57248 and closeup of the left (bottom left, from a different slice) and right (bottom right) dentary teeth 15. Dotted line represents the D15 alveolus outline, while the two individual teeth/fragments are highlighted in blue. Note that lD14 represents an articulated replacement crown, not the functional tooth. a = articular, ch = choana, lD = left dentary tooth, lM = left maxillary tooth, lP = left premaxillary tooth, m = matrix, Mg = Meckelian groove, q = quadrate, rD = right dentary tooth, s = septum, sa = surangular.**
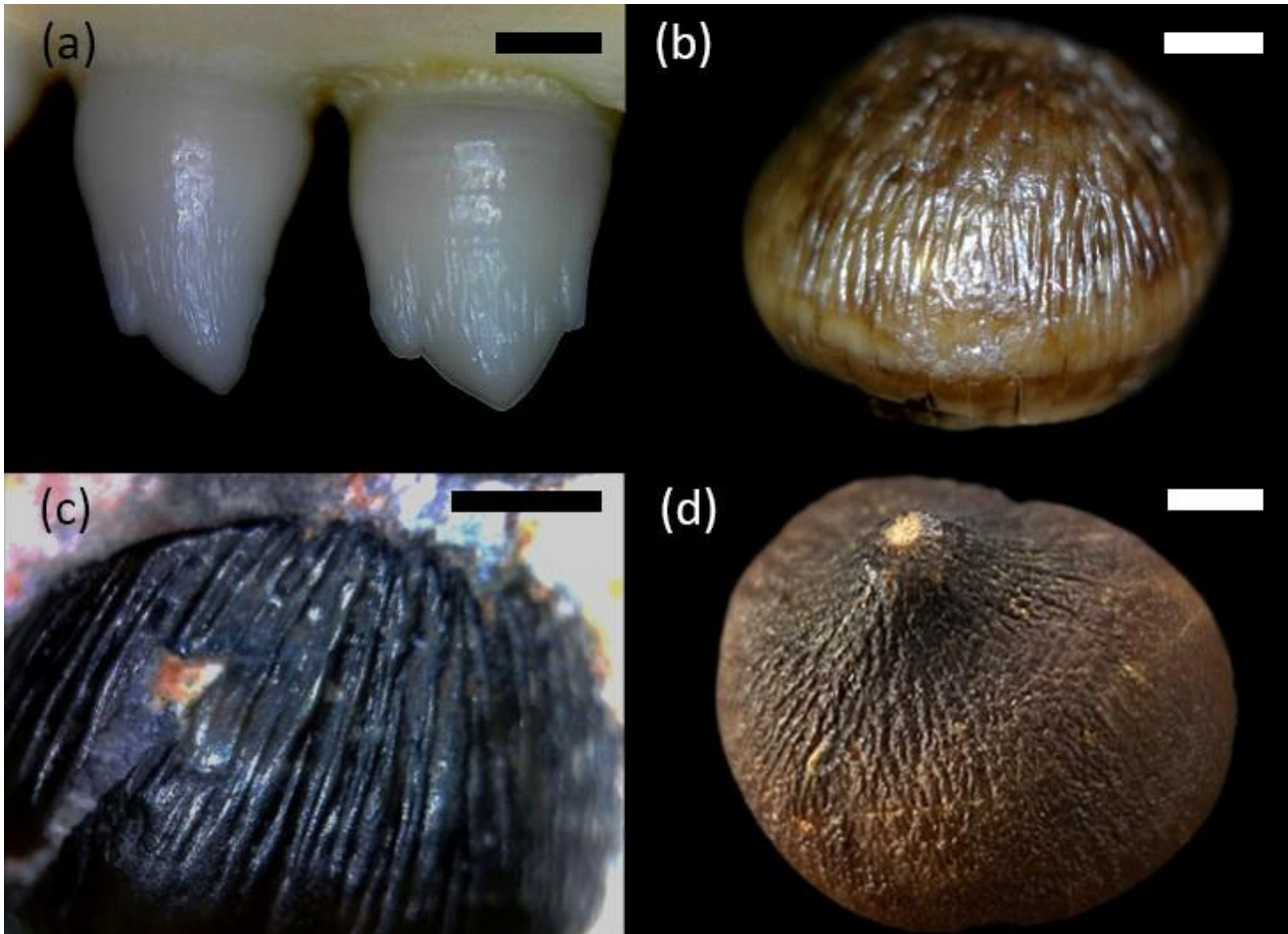
Figure S7. Four examples of enamel anastomotic wrinkling in taxa with observed or supported durophage ecologies; (a) *Salvator merianae*, scale bar = 1 mm; (b) *Brachychampsa montana*, scale bar = 1 mm; (c) Bernissartiidae indet., scale bar = 0.5 mm; (d) *Igdamanosaurus phosphaticus*, scale bar = 5 mm. Note that the *S. merianae* specimen is a subadult, still sporting the juvenile multicusped molariform morphology but already developing the adult durophage enamel ornamentation.

**Figure S8. Main text Fig. 19 (maximum recovered enamel thickness vs skull length of various living and fossil amniotes falling in the main trophic ecologies) with every represented taxon. R² values: carnivory = 0.225, specialized durophagy = 0.0024, generalist durophagy = 0.321, herbivory = 0.204, omnivory = 0.242.**
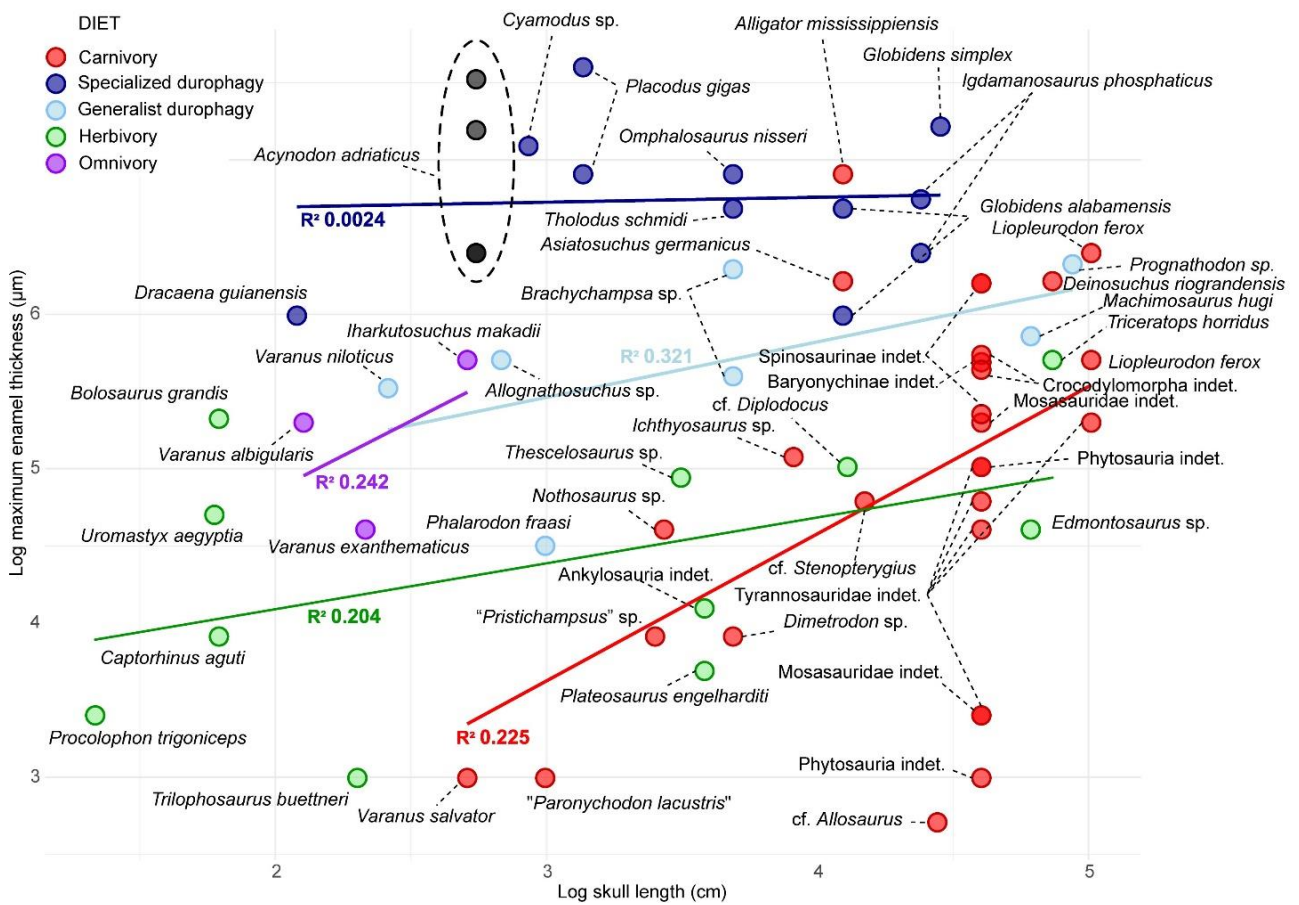
**Food processing in living molluscivorans in support of *Acynodon adriaticus* paleoecology**

Living durophagous reptiles process gastropods and other hard-shelled animals in various ways. Observing feeding individuals can reveal the diversity and common features of contemporary biomechanical adaptations. In addition to literature surveys, direct observations or accounts from breeders, and recorded feeding behaviours available from private owners and institutions, can be valuable and are herein reported.

When feeding on snails, species in the dactyloid genus *Chamelolis* (*Anolis*) deliver slow and powerful bites with simple orthal jaw closure, but with active intra-oral manipulation. Prey is repositioned several times before being crushed with multiple bites, usually unilateral unless a snail as large as the oral cavity itself is being processed. Shell fragments are removed by lingual movements before ingestion (Herrel & Holanova, 2008).

The scincids *Cyclodomorphus gerrardii* and various *Tiliqua* species exhibit an apparently simple orthal jaw closure, with minimal or absent propalinal movements. Both species crush large gastropods with slow and powerful bites, after positioning the shell between the posterior molariform teeth with repeated adjusting movements of the tongue. Anteroposterior sliding and contraction of the tongue seem to be the preferred methods for in-mouth food manipulation. Broken shell fragments are selectively removed before ingestion (Kosma, 2004; Muscioni, Pers. Obs. 2023). Substantial but more cryptic differences between the two species are likely present, but more in-depth data for the morphologically specialized *C. gerrardii* are not available.

The teiids *Dracaena guianensis* and mature *Salvator merianae* display similar dynamics, with mostly orthal jaw closure and intense anteroposterior lingual movements for rotating large gastropod shells and reorienting them between crushing power strokes. In this aspect, the more specialized *Dracaena* is slower but expectedly more efficient (Schaerlaeken et al., 2012). Vigorous and precise lingual movements sustain more intraoral transport cycles, and even large shells are rarely dropped while being processed. In contrast, *S. merianae* relies more on kinetic inertial food transport through swift movements of the cranio-cervical complex, and gastropods are dropped multiple times between bites to be consumed. At least in *Dracaena*, even relatively small broken shell fragments are selectively removed with the use of hyolingual movements before ingestion.

The varanids *Varanus niloticus* and *V. exanthematicus* display the same orthal, slow, and powerful bite dynamics. The main difference from the former squamates lies in the more frequent whole swallowing of snails after a few crushing bites (especially the smaller ones) and the prevalent use of

swift head movements and ground rubbing as intraoral adjusting methods. Tongue-based transport is present but less extensive than in teiids and scincids, probably due to their chemosensory tongues (Elias et al., 2000; Montuelle et al., 2009).

In general, the selective removal of at least relatively large shell fragments and precise oral food manipulation using either hyolingual or whole-head movements seem to be common traits among living durophagous squamates. Intra-oral food manipulation is consistent with the observations of Elias et al. (2000), shifting from purely inertial transport for gross movement of prey from the tips of the jaws into the mouth cavity to cycles of anteroposterior tongue movement for prey positioning between crushing teeth and selective shell fragment removal.

Among living crocodylians, the regular consumption of large gastropods is reported or suspected in many species (Delanie & Abercrombie, 1986; Magnusson et al., 1987; Thorbjarnarson, 1993; Horna et al., 2003; Rice, 2004; Pauwels et al., 2007; Borteiro et al., 2009; Smolensky et al., 2023), but accurate records of feeding behaviors are more difficult to gather. Descriptions of hard-shelled prey processing behaviors are scarce in the literature, and other than inferred oral food processing from museum specimens (Osi & Barrett, 2011) or a few anecdotal and video reports, in-depth data are difficult to obtain without direct access to living specimens. The crocodylian tongue is almost devoid of musculature and incapable of anteroposterior movement cycles; intra-oral food transport is therefore mediated by specialized inertial feeding (Bramble & Wake, 1985). When accepting large gastropods as offered food, captive individuals of large species (such as *Alligator mississippiensis*, *Crocodylus siamensis*, and farmed hybrids) grasp them with the anterior portion of the jaw, and the head is dorsally rotated, causing the snails to roll toward the back of the oral cavity. Before and between crushing cycles, adjustments on the blunter posterior teeth and from side to side of the mouth are achieved through rapid head and neck movements, purely by kinetic inertial transport. It is not clear if shell fragments are selectively discarded before swallowing, although the presence of shell fragments in stomach contents and breeders' observations suggest the absence of any squamate-like advanced selective behavior. In *Alligator mississippiensis*, interesting observations involve chelonivory, a common feeding habit in many populations (see among others, Delanie & Abercrombie, 1986; Rice, 2004; Saalfeld et al., 2011). When a turtle is captured, it is inertially brought to the posterior portion of the jaw, where the shell is cracked open by multiple slow unilateral bites. The turtle is repositioned after each bite through both cranio-cervical and whole-body movements and then swallowed. All living crocodylians exhibit a simple orthal jaw closure, with minimal (if any) passive propalinal motion capabilities. Additional observations of natural and experimental mollusk feeding in medium/small-sized eusuchians with tribodont posterior teeth,

whose diet naturally includes mollusks (namely *Osteolaemus* spp., *Alligator sinensis*, *Caiman latirostris*, and *Paleosuchus* spp.), would provide possibly interesting data that are currently difficult to evaluate.

The apparent bilateral symmetry of molariform replacement, on the other hand, implies that, unlike placodontians, the masticatory activity in *A. adriaticus* did not rely on periodic one-sided functional occlusion, thus supporting a side-switching dynamic not substantially different from that observed in living eusuchians. Given the size of the animal and its morphofunctional specialization, it is likely that some selection between shell fragments and soft tissue took place to some degree even in *A. adriaticus*. This could have happened with intra-oral prey manipulation, but dedicated tongue movements as seen in living *Dracaena* or *Cyclodomorphus* would imply specific adaptations of the hyolingual apparatus. These are not evident from the preserved hyoid bones of the holotype, which are not dissimilar in morphology to the usual crocodylian ones; a prominent involvement of the cranio-cervical system as observed in living varanids and eusuchians seems more likely, while the tongue was probably reduced as in living crocodiles and alligators. The relatively small size of the occipital condyle and the relative size and morphology of the cervical vertebrae might allow interesting inferences about the mobility of the cranio-cervical complex, which should be further investigated.

# REFERENCES

Arbulla, D., Caffau, M., Cucchi, F., Flora, O., Pugliese, N., Stenn, B., Tunis, G., & Zini, L. (2000). Paleoambienti Santoniano-Campaniani nell'area del Villaggio del Pescatore: la palude dell'adrosauro. In Tra Alpi, Dinaridi e Adriatico, *Atti dell'80 Riunione estiva della Società Geologica Italiana*, Trieste, 6-8 settembre 2000.

Arbulla, D., Cotza, F., Cucchi, F., Dalla Vecchia, F.M., De Giusto, A., Flora, O., Masetti, D., Palci, A., Pittau, P., Pugliese, N., Stenni, B., Tarlao, A., Tunis, G., & Zini, L. (2006): Escursione nel Carso Triestino, in Slovenia e Croazia. Stop 1. La successione Santoniano-Campaniana del Villaggio del Pescatore (Carso Triestino) nel quale sono stati rinvenuti i resti di dinosauro. Excursions guide, Società Paleontologica Italiana - Giornate di Paleontologia 2006, EUT Edizioni Università di Trieste, 20-27.

Attura, M. (1999). Aspetti Paleontologici e Geochimico-Isotopici di una successione stratigrafica Santoniana-Campaniana del Villaggio del Pescatore. Unpublished MsC thesis, Università degli Studi di Trieste. 63.

Baldassarri, L. (2024). Analisi geochimica di resti fossili e campioni geologici del Villaggio del Pescatore (Campaniano, Trieste). Master's thesis, Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Università di Bologna, 119.

Borteiro, C., Gutiérrez, F., Tedros, M., & Kolenc, F. (2009). Food habits of the Broad-snouted Caiman (*Caiman latirostris*: Crocodylia, Alligatoridae) in northwestern Uruguay. *Studies on Neotropical Fauna and Environment*, *44*(1), 31–36. https://doi.org/10.1080/01650520802507572

Bramble, D. M., & Wake, D. B. (1985). Feeding mechanisms of lower tetrapods. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake), Harvard University Press, 230-261.

Burgener, L., Hyland, E., Reich, B. J., & Scotese, C. (2023). Cretaceous climates: Mapping paleo-Köppen climatic zones using a Bayesian statistical analysis of lithologic, paleontologic, and geochemical proxies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 613, 111373. https://doi.org/10.1016/j.palaeo.2022.111373.

Chiarenza, A. A., Fabbri, M., Consorti, L., Muscioni, M., Evans, D. C., Cantalapiedra, J. L., & Fanti, F. (2021). An Italian dinosaur Lagerstätte reveals the tempo and mode 932of hadrosauriform body size evolution. *Scientific Reports*, 11(1), 23295. https://doi.org/10.1038/s41598-021-02490-x

Consorti, L., Arbulla, D., Bonini, L., Fabbi, S., Fanti, F., Franceschi, M., Frijia, G., & Pini, G. A. (2021). The Mesozoic palaeoenvironmental richness of the Trieste Karst 13, GFT 1–40. https://doi.org/10.3301/GFT.2021.06

Cucchi, F., & Piano, C. (2013). Brevi note illustrative della Carta Geologica del Carso Classico Italiano. Progetto GEO-CGT - Cartografia Geologica di sintesi in scala 1:10.000, 41.

Dalla Vecchia, F. M. (2018). A wing metacarpal from Italy and its implications for latest Cretaceous pterosaur diversity. *Geological Society*, London, Special Publications, 455(1), 209–219. https://doi.org/10.1144/SP455.1

Dalla Vecchia, F.M. (2008). I dinosauri del Villaggio del Pescatore (Trieste): qualche aggiornamento. *Atti del Museo Civico di Storia Naturale di Trieste*, 53, 111–129.

Dalla Vecchia, F.M. (2009). *Tethyshadros insularis*, a new hadrosauroid dinosaur (Ornithischia) from the Upper Cretaceous of Italy. *Journal of Vertebrate Paleontology*, 29, 1100–1116. https://doi.org/10.1671/039.029.0428

Dalla Vecchia, F.M. (2020). The unusual tail of *Tethyshadros insularis* (Dinosauria, Hadrosauroidea) from the Adriatic Island of the European archipelago. *Rivista Italiana di Paleontologia e Stratigrafia*, 126(3): 583-628. https://doi.org/10.13130/2039-4942/14075

de Winter, N. J., Müller, I. A., Kocken, I. J., Thibault, N., Ullmann, C. V., Farnsworth, A., Lunt, D. J., Claeys, P., & Ziegler, M. (2021). Absolute seasonal temperature estimates from clumped isotopes in bivalve shells suggest warm and variable greenhouse climate. *Communications Earth & Environment*, 2, 121. https://doi.org/10.1038/s43247-021-00193-9.

Delany, M. F., & Abercrombie, C. L. (1986). American Alligator Food Habits in Northcentral Florida. The Journal of Wildlife Management, 50(2), 348. https://doi.org/10.2307/3801926

Elias, J. A., Mcbrayer, L. D., & Reilly, S. M. (2000). Prey Transport Kinematics in *Tupinambis teguixin* and *Varanus exanthematicus*: Conservation of Feeding Behavior In 'Chemosensory-

Tongued' Lizards. *Journal of Experimental Biology*, 203 (4): 791–801. https://doi.org/10.1242/jeb.203.4.791

Herrel, A., & Holanova, V. (2008). Cranial morphology and bite force in *Chamaeleolis* lizards - adaptations to molluscivory? *Zoology (Jena)*, 111(6):467-75. https://doi.org/10.1016/j.zool.2008.01.002

Horna, V., Zimmermann, R., Cintra, R., & Vásquez, P. (2003). Feeding Ecology of the Black Caiman (*Melanosuchus niger*) in Manu National Park, Peru. *Lyonia*, 4(1), 65–72

Kosma R. (2004). The dentitions of recent and fossil scincomorphan lizards (Lacertilia, Squamata) - systematics, functional morphology, paleocology. PhD dissertation, Hannover (Germany): University of Hannover, p. 187. https://doi.org/10.15488/6387

Magnusson, W. E., Da Silva, E. V., & Lima, A. P. (1987). Diets of Amazonian Crocodilians. *Journal of Herpetology*, *21*(2), 85. https://doi.org/10.2307/1564468

Montuelle, S. J., Herrel, A., Schaerlaeken, V., Metzger, K. A., Mutuyeyezu, A., & Bels, V. L. (2009). Inertial feeding in the teiid lizard *Tupinambis merianae*: the effect of prey size on the movements of hyolingual apparatus and the cranio-cervical system. *Journal of Experimental Biology*, 212 (16): 2501–2510. https://doi.org/10.1242/jeb.026336

Muscioni, M., Chiarenza, A. A., Delfino, M., Fabbri, M., Milocco, K., & Fanti, F. (2023). *Acynodon adriaticus* from Villaggio del Pescatore (Campanian of Italy): Anatomical and chronostratigraphic integration improves phylogenetic resolution in Hylaeochampsidae (Eusuchia). *Cretaceous Research*, 151. https://doi.org/10.1016/j.cretres.2023.105631

Muscioni, M., Kustatscher, E., Arbulla, D., & Fanti, F. (2024). A new census of the paleodiversity of the Villaggio del Pescatore lagerstätte (Campanian, Trieste). Paleodays 2024, XXIV Edizione delle Giornate di Paleontologia, Pisa, 5-7 June 2024. Abstract book.

Nikolov, V., Dochev, D., & Brusatte, S. L. (2024). The ontogenetic status of a small hadrosauroid dinosaur from the uppermost Cretaceous of Bulgaria, and implications for the paleobiogeography and assembly of European island faunas. *Cretaceous Research*, 157, 105819. https://doi.org/10.1016/j.cretres.2023.105819.

Ősi, A., & Barrett, P. M. (2011). Dental wear and oral food processing in Caiman latirostris: Analogue for fossil crocodylians with crushing teeth. *Neues Jahrbuch Für Geologie Und Paläontologie - Abhandlungen*, *261*(2), 201–207. https://doi.org/10.1127/0077-7749/2011/0161

Palci, A. (2003): Ricostruzione paleoambientale del sito fossilifero senoniano del Villaggio del Pescatore (Trieste). Università degli Studi di Trieste, 134.

Pauwels, O. S. G., Barr, B., Sanchez, M. L., & Burger, M. (2007). Diet records for the Dwarf Crocodile, *Osteolaemus tetraspis tetraspis* in Rabi Oil fields and loango national park, southwestern Gabon. *Hamadryad*, 31. 258–264.

Rice, A.N. (2004). Diet and condition of American Alligators (*Alligator mississippiensis*) in three central Florida lakes. M.Sc. Thesis. University of Florida, 1–89.

Saalfeld, D., Conway, W. C., & Calkins, G. E. (2011). Food Habits of American Alligators (*Alligator mississippiensis*) in East Texas. *Faculty Publications*. 411. http://dx.doi.org/10.1674/0003-0031-164.1.107

Schaerlaeken, V., Holanova, V., Boistel, R., Aerts, P., Velensky, P., Rehak, I., Andrade, D. V., & Herrel, A. (2012). Built to bite: feeding kinematics, bite forces, and head shape of a specialized durophagous lizard, *Dracaena guianensis* (Teiidae). *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, *317*(6), 371–381. https://doi.org/10.1002/jez.1730

Smolensky, N. L., Fitzgerald, L., & Winemiller, K. O. (2023). Trophic Ecology of African Dwarf Crocodiles (*Osteolaemus* spp.) in Perennial and Ephemeral Aquatic Habitats. *Journal of Herpetology*, *57*(1). https://doi.org/10.1670/21-076

Tarlao, A., Tentor, M., Tunis, G., & Venturini, S. (1993). Evidences of a tectonic phase in the lower Senonian of the Villaggio del Pescatore area. *Gortania*, 15, 23-34.

Tarlao, A., Tentor, M., Tunis, G., & Venturini, S. (1995). Stop 4: Villaggio del Pescatore. *Atti del Museo Geologico e Paleontologico di Monfalcone*, Quaderno speciale 3: 135-142.

Thorbjarnarson, J. B. (1993). Diet of the Spectacled Caiman (*Caiman crocodilus*) in the Central Venezuelan Llanos. *Herpetologica*, 49(1), 108–117.