

# Osteological criteria for the specific identification of Monitor lizards (*Varanus* Merrem, 1820) remains in subfossil deposits of Sundaland and continental Southeast Asia

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**Abstract.** The identification at species level of subfossil remains of lizards from tropical regions currently suffers from strong limitation linked to the lack of comprehensive work conducted on the osteology of modern taxa. The aim of this study is to provide osteological criteria allowing for the specific identification of the subfossil remains of Sundaland and continental Southeast Asian monitor lizards (*Varanus* sp.), which are often well-represented in the deposits of this geographic area. To do so we performed an osteological study of the four species occurring in this region (*V. bengalensis* sensu lato, *V. salvator*, *V. dumerilii*, and *V. rudicollis*) using a large set of 88 skeletons of modern specimens. The observation of the full set of specimens allows us to define 41 osteological criteria distributed on 20 different anatomical parts which enable the specific identification of isolated bones of the studied species. The results highlight the importance of taking account of the morphological intraspecific variability by the use of large samples of specimens to avoid identification errors. They also show that the distinction of closely related taxa remains complex even when detailed morphological analyses are performed.

**Keywords:** morphology, osteology, paleontology, squamate, zooarchaeology.

## Introduction

In most cases, taxonomic identification of Quaternary bone subfossil remains on the basis of morphological criteria requires a comparison with skeletons of extant taxa. This process is a critical step for the two disciplines having interest in these remains, Quaternary paleontology and zooarchaeology. These research fields, however, have very different methodologies to perform the taxonomic attribution of the studied bones. Paleontologists often use systematic approaches using characters of systematic values and/or newly described criteria to reach the lowest possible taxonomic level. However, systematic data are not the core of zooarchaeological studies, which are more focused on the study

of human behaviors revealed by bone assemblages. For this reason, the identification of archaeological remains is often done using a simple visual comparison with modern taxa, and identification criteria are very rarely made available in the published studies. This makes the identification of such remains impossible to reproduce and challenge. In addition, both paleontological and zooarchaeological approaches often suffer from the lack of basic work describing the osteology of modern taxa by taking account of intraspecific and interspecific morphological variability. These issues are especially damaging in areas presenting a rich modern and subfossil biodiversity, such as tropical areas, which are often difficult and complex to study from a paleozoological point of view. To solve these problems, one must perform studies of large samples of specimens of modern taxa to describe reliable morphological criteria that allow for identification in the subfossil record. Such approaches have been already conducted on several domestic taxa of zooarchaeological interest (Zeder and Lapham, 2010; Hanot and Bochaton, 2018) and on some wild

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taxa (Pritchard, Rabett and Piper, 2009), including squamates (Bochaton et al., 2016), but much work has still to be done even for widespread and well-represented subfossil taxa.

This study attempts to fill an important gap concerning the osteology of the largest and best represented squamate taxa from prehistoric archaeological deposits of peninsular Southeast Asia and Greater Sunda islands (Auetrakulvit, 2004; Piper and Rabett, 2009, 2014; Conrad, 2015; Forestier et al., 2015; Frère et al., 2018), the monitor lizard *Varanus* Merrem, 1820. Monitor lizards, in addition to being very well-represented in archaeological deposits, are of strong interest in terms of past human behavior and paleoenvironmental studies. Indeed, because of the different ecological preferences of the *Varanus* species, archaeological remains of monitor lizards reflect both past environments and ecological niches exploited by past human populations. However, specific identification of their remains was, until now, impossible because of the lack of a proper study of the osteological morphology of the four species or complex of species (Koch et al., 2013) occurring today in peninsular Southeast Asia and Greater Sunda islands: the *bengalensis* species group, *Varanus dumerilii* (Schlegel, 1844), *V. rudicollis* (Gray, 1845), and *V. salvator* (Laurenti, 1768).

Following Böhme and Ziegler (1997) and Koch et al. (2013), the *bengalensis* group includes two terrestrial forest species presenting differences in scalation and hemipenial morphology: *Varanus bengalensis* (Daudin, 1802), and *V. nebulosus* (Gray, 1831). These two species have different ranges with *V. bengalensis* distributed in: Iran, Afghanistan, Pakistan, India, Nepal, Bangladesh, and Myanmar, and *V. nebulosus* occurring in: Myanmar, Thailand, Vietnam, peninsular Malaysia, Sumatra, and Java. However, the distinction between these two taxa is not systematically followed (e.g. Pianka and King, 2004), and several authors still considered these two “species” as subspecies of *V. bengalensis* following Auffenberg (1994). The maximal Snout-Vent Length (henceforth

SVL) recorded for *V. bengalensis* is 61 cm (Auffenberg, 1994). *Varanus dumerilii* is a monotypic species distributed in Myanmar, Thailand, peninsular Malaysia, Borneo, Sumatra, Natu, Bangka, and Biliton (Koch et al., 2013). The largest specimen ever recorded in the wild measured an SVL of 50 cm (Taylor, 1963). *Varanus rudicollis* is also a monotypic, mainly arboreal, species occurring in Thailand, Myanmar, peninsular Malaysia, Bangka, Riau, Borneo and Sumatra (Koch et al., 2013). The maximal SVL size recorded for this species is 59 cm (Lim, 1958). The last species occurring in peninsular Southeast Asia, *Varanus salvator*, is currently subdivided in five semiaquatic subspecies (*salvator*, *andamanensis*, *bivittatus*, *macromaculatus*, and *ziegleri*) distributed in Sri Lanka, Southeast Asia, Sunda islands, Sulawesi and northern Moluccas (Koch et al., 2007). This species is the largest continental modern monitor lizard with an SVL above 1 m in large adults (Pianka and King, 2004). Mertens (1942a) divided the four investigated species into two different subgenera, which are still used today: the subgenus *Empagusia* Gray, 1838 including *V. bengalensis* sensu lato, *V. dumerilii*, *V. rudicollis*, and *V. flavescens*, and the subgenus *Soterosaurus* Ziegler and Böhme, 1997 including, among other taxa, *V. salvator*. However, while molecular analyses support the notion that these two subgenera form a single clade (Ast, 2001; Vidal et al., 2012; Pyron, Burbrink and Wiens, 2013; Arida, 2017), they do not provide support for their claimed compositions, with *V. rudicollis* being closer to *V. salvator* than to the other members of *Empagusia* in some analysis (Ast, 2001; Pyron, Burbrink and Wiens, 2013).

The species *V. bengalensis* sensu lato, *V. dumerilii*, *V. rudicollis*, and *V. salvator* were previously included in several works concerning the osteology of *Varanus* (e.g. Conrad et al., 2011, 2015). As a consequence, osteological morphological differences between Asian monitor lizards were previously reported on complete skulls on the basis of morphological

descriptions (Mertens, 1942b) and Geometric Morphometric analyses (Openshaw and Keogh, 2014; Openshaw et al., 2017). However, the results of these studies are mostly unsuited to the identification of isolated skull bones and postcranial elements because they focused only on complete articulated skulls. These works also most often rely on small numbers of specimens which preclude taking account of the osteological variability of each taxon.

As the aim of this study is to provide osteological criteria allowing for the identification of isolated subfossil bone elements, we compared each cranial and postcranial bone of each taxon individually. Additionally, in order to take account of the inter- and intraspecific osteological variability, each criterion is defined on the basis of its congruent observation on a large number of comparative specimens and only the most reliable criteria are retained.

## Material and method

### *Systematic account*

Four taxa are considered in this study: *Varanus bengalensis* (Daudin, 1802), *V. dumerilii* (Schlegel, 1844), *V. rudicollis* (Gray, 1845), and *V. salvator* (Laurenti, 1768). Because the distinction between the two “species” or “subspecies” *bengalensis* and *nebulosus* is almost never made in most osteological museum collections, we had to consider these two very closely related taxa as part of the species *Varanus bengalensis*, as suggested by Auffenberg (1994). Furthermore, since the subspecific identifications of the specimens of *V. salvator* are also rarely provided in osteological museum collections, we considered these subspecies as a whole in our study. As a consequence, these two taxa are also represented by specimens collected outside of Southeast Asia (see supplementary table S1).

### *Sample of modern specimens and osteological nomenclature*

Our modern sample of *Varanus* skeletons includes 88 specimens from the Florida Museum of Natural History (UF) (Gainesville, USA), the Comparative Anatomy collection of the Muséum national d’Histoire naturelle (MNHN-ZA-AC) (Paris, France), the Phyletisches Museum (PMJ) (Jena, Germany), and Chulalongkorn University (Bangkok, Thailand). However, the four taxa were not equally represented in the visited museum institutions. As a consequence our sample mostly includes specimens of *V. bengalensis* (35) and *V. salvator* (32) with less specimens of *V. dumerilii* (13)

and *V. rudicollis* (8) (see details in supplementary table S1). All the ontogenetic stages are represented in the sample as shown by the SVL sizes of the studied specimens (see supplementary table S1).

The anatomical nomenclature used to describe the criteria is derived from that of Mertens (1942b) whose Latin terms were anglicized, and combined with the nomenclature of Evans (2008), Bahl (1937), and Ivanov et al. (2018) for anatomical structures not described by Mertens.

### *Selection of osteological criteria*

We first observed a sub-sample of ten specimens in order to describe a list of potentially useful criteria for the investigated species. This first sample was composed of skeletons of three *Varanus salvator* (UF 56617; UF 71561; MNHN-ZA-AC 1977.04), four *V. bengalensis* (UF 40387; UF 42323; UF 40386; MNHN-ZA-AC 1886.649), two *V. dumerilii* (UF 42324; UF 63821), and one *V. rudicollis* (UF 39646). All bones of the skeletons were observed, except those presenting a potentially high intraindividual variability and being difficult to characterize if isolated: phalanges, metapodials, carpal bones, tarsal bones, and caudal vertebrae. Following this first analysis, a total of 70 osteological criteria distributed amongst 29 cranial and postcranial bones were selected and tested on the full sample of specimens. Bones on which we failed to observe criteria to test include: jugal bone, transversum, coracoids, humerus, ulna, fibula, trunk vertebrae, and sacral vertebrae.

In keeping with the aim of this study to reach specific identification of fossil and sub-fossil isolated bones, we only report the criteria allowing for an unambiguous taxonomic identification of individual bones and do not consider combinations of characters from different anatomical parts. However, several criteria can occur on the same anatomical part and be used in combination to obtain fully reliable identifications. Additionally, we only report the characters we observed to be very weakly impacted by intraspecific and ontogenetic variability. Consequently, we did not consider character states occurring in less than 85% of observed specimens for a given species. However, we signaled characters that are variable in some species and not in others, considering they could still be useful in the identification process. These criteria were clearly stated as variable and were not considered as allowing for reliable taxonomic identifications.

### *Presentation of the criteria*

Each character state of each taxon is described and illustrated. The reference of each criterion in the text and supplementary material is built in the form: “abbreviation of bone name, number of the criterion – observed state”. For example, the state A of the first criteria of the premaxilla is: “PM1-A”.

In order to demonstrate the reliability of each criterion, we reported the number of specimens of the concerned species on which the character state was observed and the total number of observed specimen of that species in the

form: “number of observed character state/number of observed specimens”. Each character description is followed by: “(the reference of the criterion; the reference of the figure in which it is illustrated; the ratio of number of observed character states/number of observed specimens; the range of observed value for metrical criteria)”. The details of recorded character states on comparative specimens are reported in supplementary table S2.

## Results

### *Retained criteria*

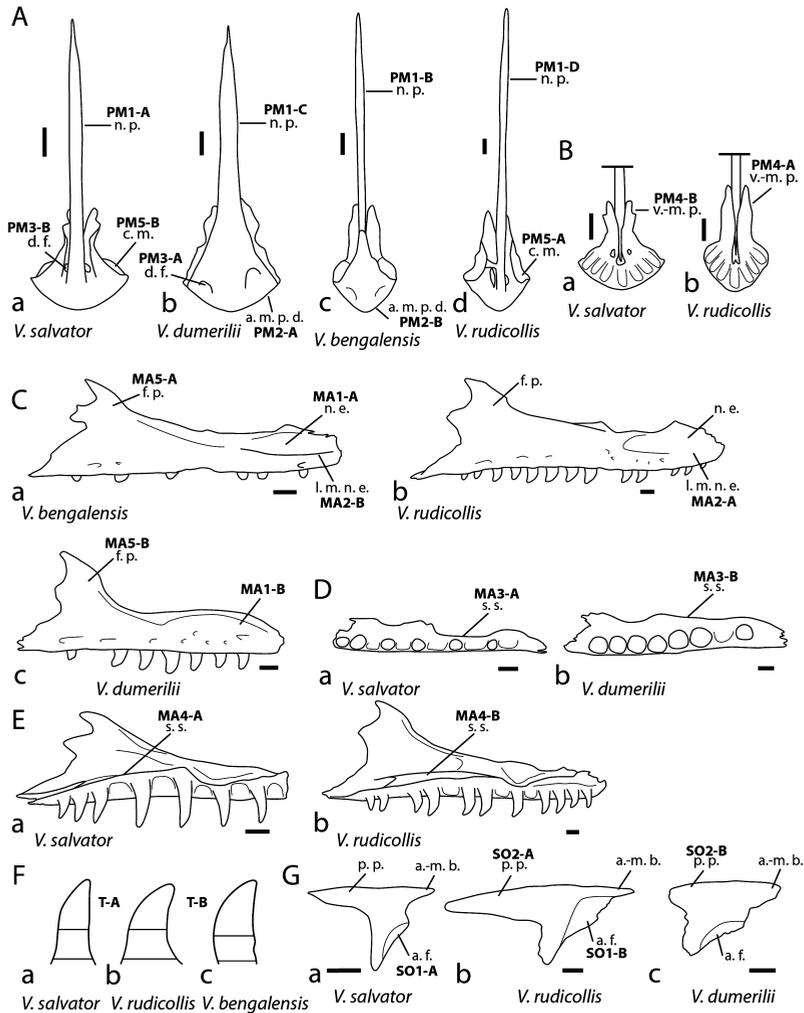
Across the testing procedure, many of the 70 criteria found as reliable on the first small set of ten specimens were found to be subject to intra and interspecific variability. As a consequence, 30 criteria were discarded and are not described thereby lowering the number of reliable criteria to 41 and the number of identifiable anatomical parts to 20 instead of 29. Non-retained criteria are presented in supplementary material S3 along with some comments on the ontogenetic variability of some bones (nasal bone, palatal bone, pterygoid, and parasphenoid).

### *Description of the diagnostic criteria*

**Premaxilla:** *V. salvator*: Nasal process with a constant width on its anterior half and a reduced posterior width (PM1-A; fig. 1A-a; 26/26), rounded anterior margin of the pars dentalis in dorsal view (PM2-A; fig. 1A-a, b; 26/26), dorsal foramen of the pars dentalis posteriorly open in dorsal view (PM3-B; fig. 1A-a; 22/25), vomero-maxillary processes posteriorly most often truncated and notched (PM4-B; fig. 1B-a; 16/24) otherwise elongated and pointed (PM4-A), contact area with the maxilla strongly reduced in dorsal view (PM5-B; fig. 1A-a; 25/25), occurrence of 7 (4/24) or 9 (20/24) tooth positions (PM6). *V. bengalensis*: Anterior part of the nasal process enlarged anteriorly and narrower posteriorly giving a triangular shape to its anterior part in dorsal view (PM1-B; fig. 1A-c; 29/30), anterior margin of the pars dentalis most often angu-

lar in dorsal view (PM2-B; fig. 1A-c,d; 14/21) otherwise rounded (PM2-A), dorsal foramen of the pars dentalis posteriorly enclosed in dorsal view (PM3-A; fig. 1A-b,c; 29/29), vomero-maxillary processes posteriorly elongated and pointed (PM4-A; fig. 1B-b; 26/27), contact area with the maxilla usually well-extended on the bone in dorsal view (PM5-A; fig. 1A-b, c, d; 21/27) otherwise reduced (PM5-B), occurrence of 7 (16/23) or 9 (7/23) tooth positions (PM6). *V. rudicollis*: Nasal process rather narrow on its whole length except at its anterior extremity above the pars dentalis (PM1-D; fig. 1A-d; 7/7), anterior margin of the pars dentalis angular in dorsal view (PM2-B; fig. 1A-c, d; 6/6), dorsal foramen of the pars dentalis either posteriorly open or enclosed in dorsal view (PM3), vomero-maxillary processes posteriorly elongated and pointed (PM4-A; fig. 1B-b; 7/7), contact area with the maxilla well-extended on the bone in dorsal view (PM5-A; fig. 1A-b, c, d; 7/7), occurrence of 9 tooth positions (PM6; 5/5). *V. dumerilii*: Nasal process wider in its anterior than in its posterior part but not strongly posteriorly reduced (PM1-C; fig. 1A-b; 12/12), rounded anterior margin of the pars dentalis in dorsal view (PM2-A; fig. 1A-a, b; 12/12), dorsal foramen of the pars dentalis posteriorly enclosed in dorsal view (PM3-A; fig. 1A-b, c; 12/12), vomero-maxillary processes rather short, posteriorly truncated and notched (PM4-B; fig. 1B-a; 13/13), contact area with the maxilla well-extended on the bone in dorsal view (PM5-A; fig. 1A-b, c, d; 12/12), 7 tooth positions (PM6; 12/12).

**Maxilla:** *V. salvator*: Occurrence of an antero-dorsal nasal excavation (MA1-A; fig. 1C-a, b; 26/26), nasal excavation presenting a blunt weakly defined lateral margin (MA2-A; fig. 1C-b; 28/28), posterior half of the supradental shelf presenting a well-marked indentation in ventral view (MA3-A; fig. 1D-a; 27/27), supradental shelf thin in medial view (MA4-A; fig. 1E-a; 27/27), facial process well-extended on the anterior part of the bone (MA5-A; fig. 1C-a, b; 27/27), in total 11-12 tooth positions (MA6;



**Figure 1.** Schemes of the osteological criteria from: premaxilla (A – antero-dorsal view; B – ventral view), maxilla (C – lateral view (right); D – ventral view (right); E – medial view (left)), teeth (F), and right supraorbital (G – ventral view). Figured specimens: *V. salvator* (UF 42905), *V. bengalensis* (UF 42323), *V. rudicollis* (UF 39646), and *V. dumerilii* (UF 63821). **Abbreviations:** a. f.: articular facet for contact with the prefrontal; a.-m. b.: antero-medial branch; a. m. p. d.: anterior margin of the pars dentalis; c. m.: contact area with the maxilla; d. f.: dorsal foramen; f. p.: facial process; l. m. n. e.: lateral margin of the nasal excavation; n. e.: nasal excavation; n. p.: nasal process; p. p.: posterior process; s. s.: supradental shelf; v.-m. p.: vomero-maxillary process. (Scale bar = 2 mm).

26/26), in lingual view, nearly conical teeth with wide base and nearly straight to posteriorly curved distal edge of the tooth crown (T-A; fig. 1F-a, b; 24/24). *V. bengalensis*: Occurrence of a nasal excavation (MA1-A; fig. 1C-a, b; 31/31), nasal excavation laterally delimited by a sharp crest (MA2-B; fig. 1C-a; 31/33), posterior half of the supradental shelf presenting a well-marked indentation in ventral view (MA3-A;

fig. 1D-a; 31/32), supradental shelf thin in medial view (MA4-A; fig. 1E-a; 29/29), facial process well-extended on the anterior part of the bone (MA5-A; fig. 1C-a, b; 33/33), in total 10-12 tooth positions (MA6; 31/31), in lingual view, nearly conical teeth with wide base and nearly straight to posteriorly curved distal edge of the tooth crown in juvenile specimens (T1-A; fig. 1F-a; 11/22) or presenting a

width in the middle of the tooth crown length wider than the base of the teeth (T-B; fig. 1F-c; 11/22). *V. rudicollis*: Occurrence of a nasal excavation (MA1-A; fig. 1C-a, b; 7/7), nasal excavation presenting a blunt and weakly defined lateral margin (MA2-A; fig. 1C-b; 7/7), posterior half of the supradental shelf either straight (2/7) or presenting a well-marked indentation (5/7) in ventral view (MA3), supradental shelf wide in medial view (MA4-B; fig. 1E-b; 7/7), facial process well-extended on the anterior part of the bone (MA5-A; fig. 1C-a, b; 7/7), in total 14-15 tooth positions (MA6; 7/7), in lingual view, nearly conical teeth with wide base and nearly straight to posteriorly curved distal edge of the tooth crown (T-A; fig. 1F-b; 7/7). *V. dumerilii*: Absence of nasal excavation (MA1-B; fig. 1C-c; 13/13), posterior half of the supradental shelf straight (MA3-B; fig. 1D-b; 13/13), supradental shelf thin in medial view (MA4-A; fig. 1E-a; 13/13), facial process short and limited to the posterior part of the bone (MA5-B; fig. 1C-c; 13/13), in total 8-9 tooth positions (MA6; 12/12), in lingual view, nearly conical teeth with wide base and nearly straight to posteriorly curved distal edge of the tooth crown (T-A; fig. 1F-b; 12/12).

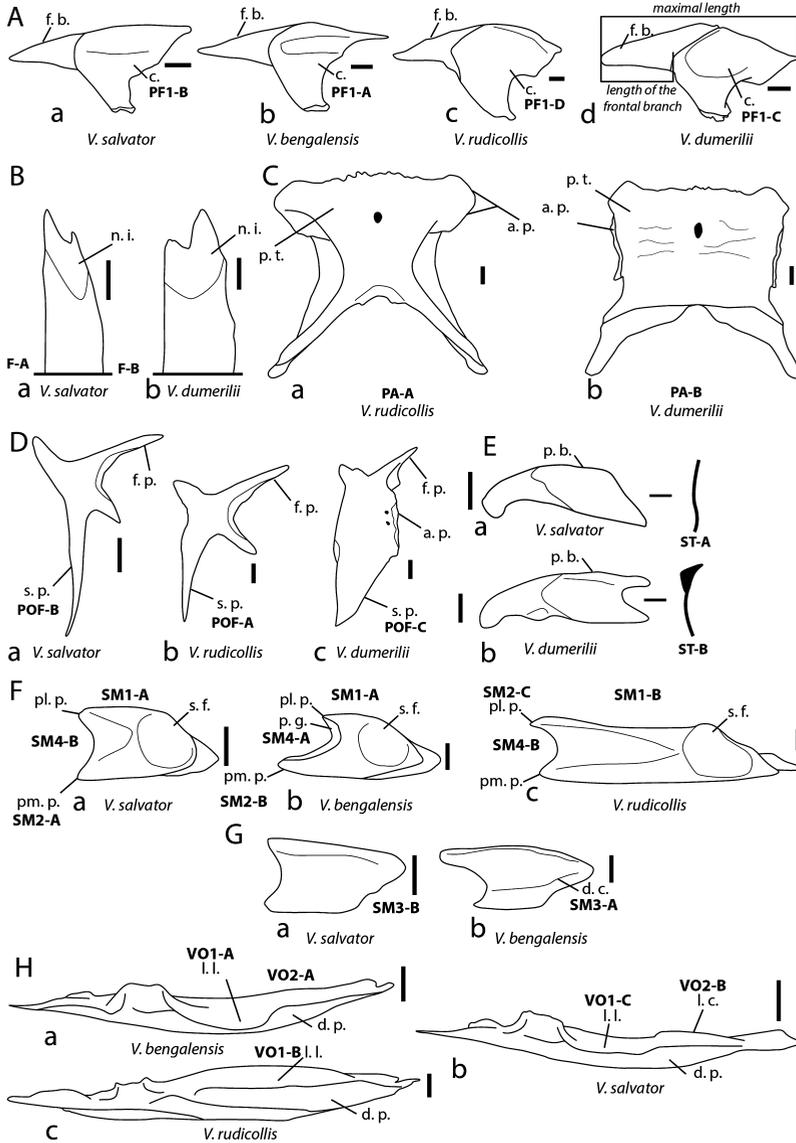
**Supraorbital:** *V. salvator* and *V. bengalensis*: articular facet for contact with the prefrontal well-delimited and exclusively situated on the antero-medial branch of the bone (SO1-A; fig. 1G-a, c; 41/41), posterior process well-developed and at least three times longer than wide (SO2-A; fig. 1G-a, b; 43/43). *V. rudicollis*: articular facet for contact with the prefrontal not well-delimited and expanded on the antero-medial branch of the bone (SO1-B; fig. 1G-b; 7/7), posterior process well-developed and at least three times longer than wide (SO2-A; fig. 1G-a, b; 7/7). *V. dumerilii*: articular facet for contact with the prefrontal well-delimited and exclusively situated on the antero-medial branch of the bone (SO1-A; fig. 1G-a, c; 11/11), posterior process very short and wider than long (SO2-B; fig. 1G-c; 12/12).

**Prefrontal:** *V. salvator*: medial surface of the conch presenting a slight horizontal crest (PF1-B; fig. 2A-a; 11/17) or is either presenting an oblong horizontal depression (PF1-B; fig. 2A-b; 2/17) or is free of any structure (PF1-D; fig. 2A-c; 4/17). *V. bengalensis*: medial surface of the conch presenting an oblong horizontal depression (PF1-A; fig. 2A-b; 18/20). *V. rudicollis*: medial surface of the conch free of any structure (PF1-D; fig. 2A-c; 5/5). *V. dumerilii*: medial surface of the conch presenting a deep sub-circular well-delimited depression (PF1-C; fig. 2A-d; 11/11), ratio between the maximal length of the bone and the length of the frontal branch below 1.96 (PF2; 11/11; 1.49–1.96). This ratio is above 1.96 for other taxa (PF2; 34/35; 1.97–2.76).

**Frontal:** *V. salvator*, *V. bengalensis*, and *V. rudicollis*: Nasal impression becomes narrow posteriorly with an axis elongated posterolaterally (F-A; fig. 2B-a; 62/63). *V. dumerilii*: posterior margin of the nasal impression sub-circular in dorsal view (F-B; fig. 2B-b; 9/11).

**Parietal:** *V. salvator*, *V. bengalensis*, and *V. rudicollis*: lateral margins more or less concave with more or less developed parietal crests and articular facets of the postorbitofrontal limited to the anterior part of the bone (PA-A; fig. 2C-a; 67/67). The morphology of the parietal varies according to the ontogeny, with the parietal crest being more and more developed and concave in larger specimens. *V. dumerilii*: bone flat with a wide parietal table lacking parietal crest, articular facets of the postorbitofrontal expanded on more than half of the lateral margin of the parietal table (PA-B; fig. 2C-b; 13/13).

**Postorbitofrontal:** *V. salvator*: squamosal process thin and at least 1.5 times longer than the frontal process (POF-B; fig. 2D-a; 27/28). *V. bengalensis*: squamosal process thin and nearly as long as the frontal process (POF-A; fig. 2D-b; 26/30). *V. rudicollis*: variable morphology of the squamosal process which can be either the same length (POF-A; 3/6) or clearly longer (POF-B; 3/6) than the frontal process. *V. dumerilii*:



**Figure 2.** Schemes of the osteological criteria from: left prefrontal (A – medial view), right frontal (B – dorsal view), parietal (C – dorsal view), left postorbitofrontal (D – dorsal view), left supratemporal (E – medial view), right septomaxilla (F – ventral view; G – dorsal view), and left vomer (H – dorso-medial view). Figured specimens: *V. salvator* (UF 42905), *V. bengalensis* (UF 42323), *V. rudicollis* (UF 39646), and *V. dumerilii* (UF 63821). *Abbreviations:* a. p.: articular facet of the postorbitofrontal; c.: conch; d. c.: dorsal crest; d. p.: drain-pipe canal; f. b.: frontal branch; f. p.: frontal process; l. c.: lateral crest; l. l.: lateral lamina; n. i.: nasal impression; p. b.: parietal branch; p. g.: posterior groove; p. t.: parietal table; pl. p.: posterolateral process; pm. p.: posteromedial fossa; s. f.: septomaxillar fossa; s. p.: squamosal process. (Scale bar = 2 mm).

squamosal process very wide and presenting an articular facet with the parietal on the anterior half of its medial side (POF-C; fig. 2D-c; 13/13).

**Supratemporal:** *V. salvator*: parietal branch taking the form of a nearly straight lamella in

anterior view (ST-A; fig. 2E-a; 15/15). *V. rudicollis*: parietal branch taking the form of a thin incurved lamella in anterior view (ST-C; 3/3). *V. bengalensis*, and *V. dumerilii*: parietal branch taking the form of a dorsally enlarged lamella in anterior view (ST-B; fig. 2E-b; 23/23).

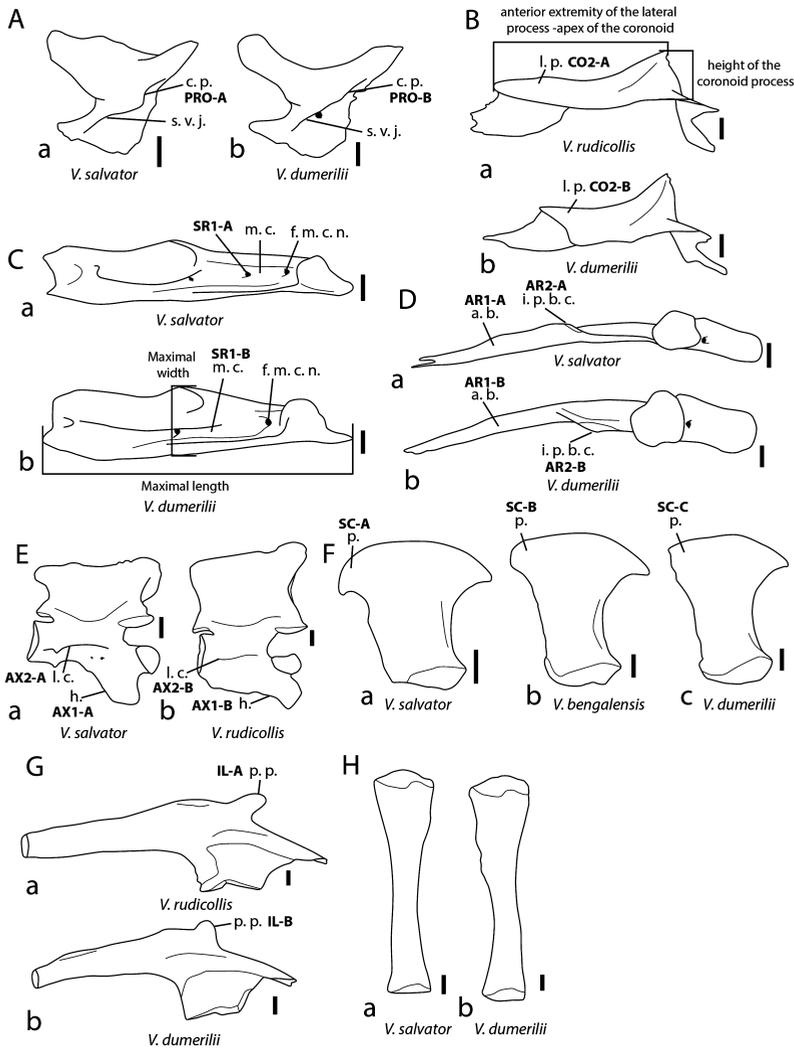
**Septomaxilla:** *V. salvator*: short posterior extension behind the septomaxillar fossa (SM1-A; fig. 2F-a, b; 22/22), posteromedial process approximately of the same length as the posterolateral process (SM2-B; fig. 2F-a; 22/22), absence of a dorsal crest on the median area of the bone (SM3-B; fig. 2G-a; 22/22), absence of posterior groove (SM4-B; fig. 2F-a, c; 22/22). *V. bengalensis*: short posterior extension behind the septomaxillar fossa (SM1-A; fig. 2F-a, b; 28/28), posteromedial process clearly longer than the posterolateral process (SM2-A; fig. 2F-b, c; 28/28), occurrence of a dorsal crest on the median area of the bone (SM3-A; fig. 2G-b; 28/28), occurrence of a deep posterior groove extending anteriorly between the ventral and dorsal surface of the posterior part of the bone (SM4-A; fig. 2F-b; 28/28). *V. rudicollis*: long posterior extension behind the septomaxillar fossa (SM1-B; fig. 2F-c; 7/7), posterolateral process clearly longer than the posteromedial process (SM2-B; fig. 2F-b, c; 6/6), absence of a dorsal crest on the median area of the bone (SM3-B; fig. 2G-a; 7/7), absence of posterior groove (SM4-B; fig. 2F-a, c; 6/6). *V. dumerilii*: short posterior extension behind the septomaxilla fossa (SM1-A; fig. 2F-a, b; 10/10), posteromedial process of variable length (SM2-A: 3/10; SM2-B: 7/10), absence of a dorsal crest on the median area of the bone (SM3-B; fig. 2G-a; 11/12), occurrence of a deep posterior groove extending anteriorly between the ventral and dorsal surface of the posterior part of the bone (SM4-A; fig. 2F-b; 10/10).

**Vomer:** *V. salvator*: lateral lamina bordering the drain-pipe canal (sensu Bahl, 1937) low and lacking a well-marked medial extension in dorso-lateral view (VO1-C; fig. 2H-b; 16/16), antero-lateral margin presenting a well-marked lateral crest in dorso-lateral view (VO2-B; fig. 2H-b; 15/15). *V. bengalensis*: lateral lamina bordering the drain-pipe canal low but presenting a well-marked medial extension restricted to the median part of the bone and partially covering the drain-pipe canal (VO1-A; fig. 2H-a;

27/27), antero-lateral margin most often lacking a well-marked lateral crest in dorso-lateral view (VO2-A; fig. 2H-a; 13/19) but not systematically (VO2-B; fig. 2H-b; 6/19). *V. rudicollis*: lateral lamina bordering the drain-pipe canal high on its whole length and slightly curved in medial direction in dorso-lateral view (VO1-B; fig. 2H-c; 7/7). *V. dumerilii*: lateral lamina bordering the drain-pipe canal usually low and lacking a well-marked medial extension in dorso-lateral view (VO1-C; fig. 2H-b; 7/10) but occurrence of medial extension on some specimens (VO1-A; fig. 2H-b; 3/10), antero-lateral margin lacking a well-marked lateral crest in dorso-lateral view (VO2-A; fig. 2H-a; 10/10).

**Prootic:** *V. salvator*, *V. bengalensis*, and *V. rudicollis*: occurrence of a posterior extension of the crista prootica bordering the sulcus venae jugularis (PRO-A; fig. 3A-a; 56/60). *V. dumerilii*: absence of a posterior extension of the crista prootica bordering the sulcus venae jugularis making the anterior margin of the crista prootica straight in lateral view (PRO-B; fig. 3A-b; 13/13).

**Dentary:** *V. salvator*: 11 or 12 dental positions (D; 24/26), rarely 13 dental positions (D; 2/26), in lingual view, nearly conical teeth with wide base and nearly straight to posteriorly curved distal edge of the tooth crown (T-A; fig. 1F-a, b; 24/24). *V. bengalensis*: 11 or 12 dental positions (D; 32/32), in lingual view, nearly conical teeth with wide base and nearly straight to posteriorly curved distal edge of the tooth crown in juvenile specimens (T1-A; fig. 1F-a; 11/22) or presenting a width in the middle of the tooth crown length wider than the base of the teeth (T-B; fig. 1F-c; 11/22). *V. rudicollis*: 13 dental positions (D; 6/6), in lingual view, nearly conical teeth with wide base and nearly straight to posteriorly curved distal edge of the tooth crown (T-A; fig. 1F-b; 7/7). *V. dumerilii*: 10 dental positions (D; 11/11), in lingual view, nearly conical teeth with wide base and nearly straight to posteriorly curved dis-



**Figure 3.** Schemes of the osteological criteria from: left prootic (A – lateral view), left coronoid (B – lateral view), right surangular (C – medial view), right articular (D – dorsal view), axis (E – lateral view), left scapula (F – lateral view), right ilium (G – right lateral view), and right tibia (H – ventral view). Figured specimens: *V. salvator* (UF 42905), *V. bengalensis* (UF 42323), *V. rudicollis* (UF 39646), and *V. dumerilii* (UF 63821). *Abbreviations:* a. b.: anterior branch; c. p.: crista prootica; f. m. c. n.: foramen for the mandibular cutaneous nerve; h.: hypapophyse; i. p. b. c.: imprint of the posterior branch of the coronoid; l. c.: lateral crest; l. p.: lateral process; m. c.: mandibular canal; p.: proscapulum; p. p.: preacetabular process; s. v. j.: sulcus venae jugularis. (Scale bar = 2 mm).

tal edge of the tooth crown (T1-A; fig. 1F-b; 12/12).

**Coronoid:** *V. salvator* and *V. bengalensis*: ratio: distance between the anterior extremity of the lateral process and the apex of the coronoid/greatest height of the coronoid process above 3.35 (CO1; 5/6; 3.17-3.83), anterior extremity of the lateral process pointed (CO2-A; fig. 3B-a; 7/7). *V. dumerilii*: ratio: distance between the anterior extremity of the lateral process and the apex of the

fig. 3B-a; 55/55). *V. rudicollis*: ratio: distance between the anterior extremity of the lateral process and the apex of the coronoid process above 3.35 (CO1; 5/6; 3.17-3.83), anterior extremity of the lateral process pointed (CO2-A; fig. 3B-a; 7/7). *V. dumerilii*: ratio: distance between the anterior extremity of the lateral process and the apex of the

coronoid/greatest height of the coronoid process below 2.6 (CO1; 13/13; 1.98-2.5), anterior extremity of the lateral process truncated (CO2-B; fig. 3B-b; 13/13).

**Surangular:** *V. salvator*, *V. bengalensis*, and *V. rudicollis*: occurrence of at least one foramen situated anteriorly to the foramen for the mandibular cutaneous nerve in the posterior part of the mandibular canal (SR1-A; fig. 3C-a; 35/36), ratio between the maximal length and the maximal width of the bone above 4.66 (SR2; 30/35; 4.19-5.8). *V. dumerilii*: absence of foramen situated anteriorly to the foramen for the mandibular cutaneous nerve in the posterior part of the mandibular canal (SR1-B; fig. 3C-b; 7/7), ratio between the maximal length and the maximal width of the bone below 4.66 (SR2-A; 9/10; 3.73-5.0).

**Articular:** *V. bengalensis*, *V. salvator*, and *V. rudicollis*: lateral margin of the anterior branch straight to slightly curved in medial direction (AR1-A; fig. 3D-a; 57/59), imprint of the posterior branch of the coronoid on the medial blade weakly marked and weakly posteriorly extended (AR2-A; fig. 3D-a; 39/40). *V. dumerilii*: lateral margin of the anterior branch curved in medial direction (AR1-B; fig. 3D-b; 12/13), imprint of the posterior branch of the coronoid on the medial blade strongly marked and posteriorly well-extended (AR2-B; fig. 3D-b; 10/10).

**Axis:** *V. salvator*: Variable morphology of the hypapophysis in lateral view from curved (AX1-B; fig. 3E-a; 15/22) to straight (AX1-A fig. 3E-b; 7/22), lateral crest of the centrum thin with a small triangular lateral extension (AX2-A; fig. 3E-a; 23/24). *V. bengalensis*, and *V. dumerilii*: hypapophyse curved in lateral view (AX1-B; fig. 3E-a; 42/42), lateral crest of the centrum weakly marked and lacking lateral extensions (AX2-B; fig. 3E-b; 39/41). *V. rudicollis*: hypapophyse straight in lateral view (AX1-A; fig. 3E-b; 6/6), lateral crest of the centrum weakly marked and lacking lateral extensions (AX2-B; fig. 3E-b; 6/6).

**Scapula:** *V. salvator*: occurrence of a hook shaped anterior projection of the proscapulum

(SC-A; fig. 3F-a; 25/25). *V. bengalensis* and *V. rudicollis*: occurrence of a blunted anterior projection of the proscapulum (SC-B; fig. 3F-b; 39/39). *V. dumerilii*: absence of an anterior projection of the proscapulum (SC-C; fig. 3F-c; 12/13).

**Ilium:** *V. salvator*, *V. rudicollis* and *V. bengalensis*: preacetabular process pointed and oriented in posterior direction (IL-A; fig. 3G-a; 59/64). *V. dumerilii*: preacetabular process rounded, flattened and oriented in dorsal direction (IL-B; fig. 3G-b; 13/13).

**Pubis:** *V. salvator*, and *V. rudicollis*: ratio between the maximal length and the distal height of the bone between 2.0 and 2.8 (PU; 33/33). *V. bengalensis*, and *V. dumerilii*: Ratio between the maximal length and the distal height of the bone between 2.9 and 4.1 (PU; 42/44).

**Tibia:** *V. salvator*, *V. rudicollis* and *V. bengalensis*: diaphysis more or less straight in lateral view (TI-A; fig. 3H-a; 56/60). *V. dumerilii*: diaphysis sinusoidal in lateral view (TI-B; fig. 3H-b; 11/11).

## Discussion

Our results show that an unambiguous identification of the four studied taxa is possible on only six different anatomical parts (premaxilla, maxilla, prefrontal, septomaxilla, vomer and dentary) among the 29 bones originally investigated. However, *V. dumerilii* was presenting many specific osteological character states allowing for its identification on 18 of the 20 anatomical parts on which reliable criteria were found. The osteological morphology of the three other taxa was, in comparison, more homogenous although several bones present specific criteria of each of the four taxa. In addition to character states particular to a species, some criteria, although not being characteristic of a single species, can still be useful in specific cases. These criteria can, for instance, be useful for the identification of a complete skeleton or of a bone assemblage in which specific

**Table 1.** Table summarizing the potential of each individual bone in terms of taxonomic identification. A “X” indicates that the taxon can be unambiguously identified using the corresponding bone. Grey levels indicate a character state similar for at least two taxa. Two levels of grey on the same row indicate two different character states shares by different taxa. Two levels of grey in a single cell indicate that two states can occur on a single taxon.

Bone/Taxon	<i>V. bengalensis</i>	<i>V. salvator</i>	<i>V. rudicollis</i>	<i>V. dumerilii</i>
Premaxilla	X	X	X	X
Maxilla	X	X	X	X
Supraorbital	[Grey]		X	X
Prefrontal	X	X	X	X
Frontal	[Grey]			X
Parietal	[Grey]			X
Postorbitofrontal	[Grey]	[Grey]	[Grey]	X
Supratemporal	[Grey]	X	X	[Grey]
Septomaxilla	X	X	X	X
Vomer	X	X	X	X
Prootic	[Grey]			X
Dentary	X	X	X	X
Coronoid	[Grey]		X	X
Surangular	[Grey]			X
Articular	[Grey]			X
Axis		X	X	
Scapula	X	[Grey]		X
Ilium	[Grey]			X
Pubis	[Grey]			[Grey]
Tibia				X

criteria have already demonstrated the predominance of one or more taxa. For instance, the criterion recorded on the pubis shared between *V. bengalensis* and *V. dumerilii* could be considered as an argument for the occurrence of *V. bengalensis* in the case the other remains do not present at least one of the numerous specific character states of *V. dumerilii*. The potential of each anatomical part in terms of specific identification of isolated bones are summarized in table 1. These criteria can be applied to every individual and are robust to intraspecific variability should it be ontogenetic morphological variability or sexual dimorphism.

Although allowing for the identification of some of the anatomical parts of the investigated taxa, our results shows the absence of observed morphological differences on most skeletal elements which highlight the strong morphological similarities between the four studied species. This observation is congruent with the phylogenetic data indicating that observed taxa are part of the same *Varanus* clade. The results also

demonstrate the importance of taking intraspecific variability into account in anatomical studies looking for minor osteological criteria useful in separating closely related taxa. Indeed, nearly half (33) of the 70 characters retained during our first observations have been demonstrated to be subject to intraspecific variability, therefore, useless for taxonomic identification. This highlights the major bias potentially impacting every anatomical study using very few (if not a single) specimens in their analyses. In the case of lizards, this bias could be a possible explanation for the differences observed between molecular phylogenies (Ast, 2001; Vidal et al., 2012; Pyron, Burbrink and Wiens, 2013; Arida, 2017) and phylogenies constructed on the basis of osteological characters (Conrad, Balcarcel and Mehling, 2012; Ivanov et al., 2018). Indeed, although molecular phylogenies appear to be relatively uniform, published analysis using osteological characters and integrating fossils present more or less strong differences with the latter. In addition, morphological differences

can sometimes contradict phylogenetic relationships established on the basis of molecular data. Our study provides an example of this. Indeed, our recorded osteological criteria show that *V. dumerilii* present far less common traits (between 4 and 7 depending on the taxa) with the three other taxa than these taxa between them (between 16 and 17 depending on the taxa). In the molecular phylogenies (Pyron, Burbrink and Wiens, 2013), *V. dumerilii* is however closer to *V. bengalensis* than to the other taxa. Concerning more specific aspects, our observations contradict those of Conrad et al. (2012) regarding at least their characters “83” and “94” but we did not assess the full set of characters recorded by these authors. Following our observations, character “83” of Conrad et al. (2012): “occurrence and development of a parietal nuchal fossa”, is variable (0 or 1) in *V. bengalensis* and not strictly absent (0). Additionally, character “94”: “fusion of postorbitofrontal”, is present (1) in the four investigated taxa.

From a global point of view, our results demonstrate the difficulties in correctly identifying Southeast Asian monitor lizards in subfossil contexts. Indeed, among the few anatomical parts found to be useful for taxonomic identification, most are fragile and/or small elements rarely found in the deposits and need to be complete in order to be identified. The lack of criteria on the largest and sturdiest anatomical elements, especially limb bones and vertebrae, precludes the specific identification of most of the bone remains from subfossil deposits. Other, more time consuming methodologies like geometric morphometrics (Openshaw et al., 2017) or ancient DNA analysis could however be applied to attempt an identification of these remains. On a more positive note, the osteological criteria we describe will allow for the first reliable specific identification of *Varanus* isolated remains in Southeast Asia. This will constitute an important step forward in the study of the past distribution of these lizards but also of the behavior of past human populations that were hunting these lizards (Auetrakulvit, 2004;

Forestier et al., 2015; Frère et al., 2018). Our results also highlight the difficulty in obtaining specific identification using isolated fossil remains even when careful osteological analyses were previously conducted on modern relatives. This shows how important it is to avoid deterministic identification while lacking strong support in order to avert errors and diffusion of erroneous data.

This work is only a first step toward the study of subfossil Southeast Asian squamates. Much work remains to be done in order to be able to identify the highly diverse monitor lizards occurring in, for instance, the Philippines and Sulawesi. More generally, further osteological studies still have to be performed on modern taxa in order to obtain satisfactory identification of ancient squamates in this region. Indeed, the osteology of most taxa is still unknown and, as a consequence, squamate subfossil remains are currently of almost no use in the study of the evolution of past biodiversity, past environments, and past human behaviors, despite being well-represented in the subfossil deposits of Southeast Asia. This issue is however not specific to the latter and also impacts other areas, such as Europe (Villa et al., 2017), that are considered as better known from the paleontological point of view (see also Bell and Mead (2014) for general discussion about the poor knowledge of the osteology of extant taxa).

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**Supplementary material.** Supplementary material is available online at:

<https://figshare.com/s/8fe6de910f38d76bedd7>

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