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| **RESEARCH ARTICLE**

Potential Evolutionary Convergence in Trophic Adaptations of Two Booidean Snake Lineages as Evidenced by Skull Morphology

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ABSTRACT
Booidean snakes are a diverse and widespread lineage with an intriguing evolutionary and biogeographic history. By means of cranial morphology and osteology, this study investigates the evolutionary convergence in the Neotropical genera *Boa* and *Corallus* on the one hand and the Malagasy clade comprising *Acrantophis* and *Sanzinia* on the other. We hypothesize that the mostly arboreal *Corallus* and *Sanzinia* present larger jaws and longer teeth to keep hold of the prey and resist gravity and torsional forces acting on their skull while hanging from branches, while terrestrial genera such as *Acrantophis* show thinner jaws with shorter teeth because they can rely on the full length of their coils to immobilize and constrict the prey together with a substrate that supports the whole of their body. Overall, we highlight how booidean snakes can serve as intriguing subjects for the study of contingency, determinism, and opportunity in the evolution of distant lineages both phylogenetically and geographically. We also provide the first complete description of the skull of *Boa constrictor*.

1 | Introduction

The superfamily Booidea is an ancient lineage of non-venomous snakes displaying exceptional evolutionary and ecological diversity. Its members include some of the largest snakes on the planet, such as the 6-m long green anaconda (*Eunectes murinus*), alongside others that do not exceed 50 cm in length (Reynolds, Niemiller, and Revell 2014). Furthermore, booideans occupy virtually all ecosystems in the (sub)tropical belt and are ecomorphologically diverse, ranging from arboreal ambush predators like the American tree boas (genus *Corallus*) to the desert-dwelling fossorial sand boas (genus *Eryx*). The biogeography of this superfamily is especially curious, as although the majority of the clade is native to South and Central America, individual genera within the

booidean tree (*Calabaria*, *Candoia*, and *Eryx*) are distributed in Africa, southern Europe, the Middle East, and Melanesia and Micronesia (Reynolds, Niemiller, and Revell 2014; Noonan and Chippindale 2006). The presence of booidean snakes in Madagascar, an island located more than 1000 km away from the closest native range of any other member of this superfamily, is particularly puzzling, and therefore presents interesting insights into the evolution of these snakes.

The taxonomy and systematics of Madagascan boas (family Sanziniidae Romer, 1956) has been a matter of discussion since their first descriptions in the 19th century. Four species of boas, grouped in two genera, are currently recognized in Madagascar: the genus *Acrantophis* includes *Acrantophis madagascariensis* (Duméril and Bibron 1844) and *A. dumerili* Jan, 1860, while the

genus *Sanzinia* consists of *Sanzinia madagascariensis* (Duméril and Bibron 1844) and *S. volontany* Vences and Glaw 2003. The latter was first described as a subspecies of *S. madagascariensis*, but the remarkable genetic distance between the two snakes shown by molecular analysis (almost twice as great as that between the two *Acrantophis* species) led to its elevation to full species level (Reynolds, Niemiller, and Revell 2014; Vences et al. 2001; Vences and Glaw 2003). Although the two *Sanzinia* species differ somewhat in coloration (adults of *S. volontany* are generally brown whereas *S. madagascariensis* tend to be more clearly green) and marginally in a few pholidotic characters (Vences and Glaw 2003), a detailed modern analysis of their morphological differences was never undertaken, and the two sometimes remain difficult to distinguish.

Given their overall morphological similarity, it was long thought that Madagascan boas were closely allied with those of Central and South America. Indeed, Boulenger was the first to synonymize *Sanzinia* with *Corallus* due to their apparent superficial similarities (Boulenger 1893). Both genera comprise mostly arboreal and nocturnal species (Pizzatto and Marques 2007a; Pizzatto, Almeida-Santos, and Shine 2007b). Furthermore, both genera have distinctly enlarged heads and labial pits or grooves, which are thermosensitive in *Corallus* but may not be in *Sanzinia* (Maderson 1970). More recently, Kluge (1991) found sufficient shared characters in cranial morphology between Madagascan booideans and *Boa constrictor* to suggest that they might be congeners, and moved them all into *Boa*. Notably, the skull of *Sanzinia* was described extensively in a French monography by Genest-Villard (1966) but was neglected by subsequent workers, despite its obvious relevance for systematics efforts.

The synonymy of Madagascan booideans with *Boa* and/or *Corallus* has since been resoundingly rejected on molecular phylogenetic grounds (Figure 1), to the point where the two clades are now part of different families: Sanziniidae for the Malagasy lineage and Boidae for the two Neotropical genera (Burbrink 2005; Figueroa et al. 2016; Noonan and Chippindale 2006; Pyron, Burbrink, and Wiens 2013; Pyron, Reynolds, and Burbrink 2014; Raxworthy and Glaw 2022; Vences et al. 2001). In fact, several studies have found the Sanziniidae to be instead allied with the unusual burrowing booidean *Calabaria reinhardtii* from central Africa (Reynolds, Niemiller, and Revell 2014; Noonan and Sites 2010; Orozco-Terwengel et al. 2008), which had been considered an erycine boa by Kluge (1993) but is now placed in its own family, Calabariidae Gray, 1858 (Pyron, Burbrink, and Wiens 2013; Pyron, Reynolds, and Burbrink 2014). However, the position of *Calabaria* itself within the Booidea remains unresolved (Figueroa et al. 2016).

The hypothesis that Madagascar's booideans may be more closely related to an aberrant African fossorial species than to their South American ecomorphological homologs points toward a morphological convergence within the superfamily Booidea. This phenomenon was also reported in Pythonoidea, the sister group to booideans, equally characterized by considerable disparities in size and morphology across members of the clade (Esquerré and Keogh 2016; Esquerré, Sherratt, and Keogh 2017). Speculations and/or investigations of an influence of ecological selection pressures on the morphology of snake skulls date back to early studies on the topic (Frazzetta 1966, Genest-Villard 1966). Natural selection favoring similar eco-morphological cephalic traits in distantly related species has been postulated both within Booidea/Pythonoidea (Pizzatto, Almeida-Santos, and Shine 2007b; Esquerré and Keogh 2016) and in other distantly related snake clades (Deepak, Gower, and Cooper 2022; Fabre et al. 2016; Sherratt et al. 2019; Strong, Scherz, and Caldwell 2022) on the basis of morphometric observations.

More specifically, *Boa* (and thus likely *Acrantophis* too) falls within the semiarboreal morphotype of Esquerré and Keogh (2016), characterized by a streamlined head and eyes shifted dorsally; while, *Corallus* (and likely *Sanzinia* as well) clusters within the arboreal morphotype, with funnel-shaped heads and markedly lateral eyes (Esquerré and Keogh 2016). Furthermore, specialized labial scales in *Sanzinia* and *Corallus* but not in *Boa* and *Acrantophis* (Lynn 1931; Ros 1935; von Düring 1974) reinforces a scenario of selection pressures related to ecology (e.g., foraging) favoring certain anatomical features over others irrespective of phylogenetic factors.

In this study, we compare the morphology of the skulls of Madagascan booideans (both *Sanzinia* and both *Acrantophis*
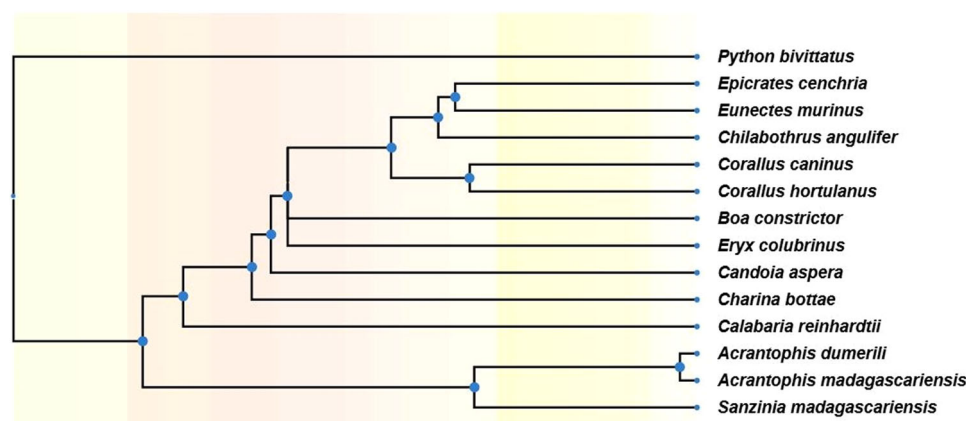

FIGURE 1 | Phylogeny of representative booideans. Note the distant relationship between the Sanziniidae and *Boa constrictor*, which is instead more closely related to *Corallus*. Tree obtained from timetree.org.

species) with that of selected Neotropical booideans (*Corallus caninus* and *B. constrictor*), to establish the extent of morphological convergence between Madagascan and Neotropical booideans originating from the influence of similar ecological guilds. As part of this endeavor, we also report the first complete cranial description for *B. constrictor*, despite it being one of the most widely known and extensively studied snake species. Finally, we include a review of available data on the diets and foraging habits of Madagascan boas and two representative Neotropical species, *C. caninus* and *B. constrictor*.

2 | Materials and Methods

Dietary records were assembled from the scientific literature (books and peer-reviewed papers) as well as by searching the citizen science database of iNaturalist (http://www.inaturalist.org) and the Facebook groups "Wild snakes: Predators and prey" and "Wild snakes: Predation records." For Facebook data, only reports of predation events accompanied by clear photographic evidence of the species and act in question were included. Both groups have been active for several years and are managed by accredited experts, which ensures proper screening of content and accurate identifications.

For this dietary analysis, *S. madagascariensis* and *S. volontany*, as well as *Boa imperator* and *B. constrictor*, were regarded as single entities because they were only recently recognized as species-level units (Hynková, Starostová, and Frynta 2009; Vences and Glaw 2003) and the literature from before these nomenclatural changes does not adequately distinguish between them. The same rationale was applied to *C. caninus* and the more recently described *C. batesii*, which are nearly identical in morphology and were split only recently (Henderson, Passos, and Feitosa 2009). Reports of feeding in captive animals were excluded from the analysis. Dietary records for the Amazon tree boa (*Corallus hortulanus*) were also included due to the paucity of information available for *C. caninus* alone. Importantly, *C. caninus* and *C. hortulanus* are not perfect ecological nor morphological homologs (Henderson, Pauers, and Colston 2013), but scarcity of data on the closest ecomorphological relatives of *C. caninus* (*C. batesii* and *C. cropanii*) restricted our options. All records obtained in this study

were then visualized graphically by species in GraphPad Prism v. 10.0.3.

Six specimens belonging to six different booidean species (Table 1) were selected from the Zoologische Staatssammlung München (ZSM) collection. Skull morphology was assessed from microcomputed Tomography (micro-CT) scans. Each specimen was placed in a container selected to fit its size and was held stable by inserting polystyrene layers to fill the gaps between the container's surface and the animal itself. Seventy percent ethanol was added to prevent desiccation by saturating the air in the container with alcohol during the scan. Subsequently, the container was hermetically sealed. Scanning was conducted using a phoenix|x nanotom m (GE Measurement & Control, Wunstorf, Germany), with scan settings optimized for each specimen depending on its size. Scans were reconstructed as 16-bit volume files in datos|x reconstruct (GE Measurement & Control) and converted to 8-bit following histogram adjustment in VG Studio Max 2.2 (Volume Graphics GmbH, Heidelberg, Germany). Scan data were visualized in this software using the Phong renderer and a custom preset. Screenshots of the scans were produced using the image capture function. Osteological examination was conducted on these videos and volume renderings, following recommendations by Scherz et al. (2017). Segmentation for figure production was conducted in Amira 6.0 (FEI Visualization Sciences Group, Bordeaux, France). Scans and their derived files are deposited in MorphoSource at the following URL: https://www.morphosource.org/Detail/ProjectDetail/Show/project_id/522.

Osteological terminology follows Kluge (1991, 1993), Frazzetta (1959, 1966), Underwood (1976), McDowell (2008), and Cundall and Irish (2008).

3 | Results

3.1 | Dietary Notes

We found a total of 618 dietary records in the literature for *Sanzinia* (both species combined, $n = 11$), *A. dumerili* ($n = 8$), *A. madagascariensis* ($n = 10$), *B. constrictor* (including *B. imperator*; $n = 525$), *C. caninus* ($n = 10$), and *C. hortulanus* ($n = 64$)

TABLE 1 | List of species analyzed in this study and number of specimens used. Voltage (kV) and resistance (μA) settings employed during the micro-CT scanning are reported together with the number of projections generated for each specimen. Exposure time in ms is included as well.

Specimen number	Species	Age	kV	μA	Projections	Timing (ms)	MorphoSource Media
ZSM 805/2001	*Acrantophis madagascariensis*	Adult	140	200	2440	750	000087609
ZSM 949/2003	*Acrantophis dumerili*	Adult	140	120	2440	750	000087521
ZSM 24/1971	*Boa c. constrictor*	Adult	180	80	2440	750	000087607
ZSM 1115/2003	*Sanzinia madagascariensis*	Adult	140	140	2440	750	000087610
ZSM 67/2006	*Sanzinia volontany*	Subadult	140	80	2440	750	000087611
ZSM uninventoried	*Corallus caninus*	Adult	140	80	2440	750	000087612

as of October 2023. In the case of the genus *Acrantophis*, which is almost exclusively terrestrial, only one report of arboreal foraging (Love 2004) was found. Conversely, *B. constrictor* was extensively observed hunting and/or swallowing prey both on trees and on the ground. *Corallus* was documented to hunt exclusively in trees (although most records do not mention the setting where predation occurred), while *Sanzinia*, although generally considered a "tree boa" (Pizzatto and Marques 2007a; Pizzatto, Almeida-Santos, and Shine 2007b), has been observed foraging on the ground on one occasion.

The main prey type for *Acrantophis* appears to be mammals, especially tenrecs, rodents and lemurs. *A. madagascariensis*, being considerably larger than *A. dumerili*, more often preys on lemurs, while the latter prefers smaller prey. Occasional predation on lizards (by *A. madagascariensis*), birds (both species) and even invertebrates (by *A. dumerili*) was documented. Both *B. constrictor* and *A. madagascariensis* hunt primates and other large-sized prey on a regular basis, as well as smaller mammalian taxa such as rodents. However, *B. constrictor* is more generalistic, frequently feeding on birds and lizards as well. *Corallus caninus* and *Sanzinia* appear to prefer mammals, with birds and other reptiles apparently featuring only in a minor fraction of dietary observations. This contrasts with *C. hortulanus*, whose diet includes a preponderant percentage of birds. Our findings on the feeding habits of all analyzed species are summarized in Figure 2, while the underlying data are presented in Supporting Information S2: Table 1.

3.2 | Osteological Description

We here describe each bone of the skull in general terms first, then compare across the four different genera examined in this study (*Acrantophis* vs. *Sanzinia* vs. *Boa* vs. *Corallus*) and ultimately compare at the species level for the two Madagascan genera (*A. madagascariensis* vs. *A. dumerili*, *S. madagascariensis* vs. *S. volontany*). Side-by-side illustrations of each skull in lateral, dorsal, and ventral view are shown in Figures 3 and 4. As osteological data from *S. volontany* is only available from a subadult specimen, we err on the side of caution in highlighting differences between it and its sister species. Overall, the *B. constrictor* skull was the largest at 83 mm in length (snout to neck) and 47.5 mm in width (measured as the distance between the dorsal ends of the compound bones). *Corallus caninus* was second (59.5 mm length, 38 mm width), followed by *A. madagascariensis* (57 mm length, 30 mm width) and *A. dumerili* (42 mm length, 23 mm width). Finally, *S. madagascariensis* (38 mm length, 30 mm width) and *S. volontany* (38.5 mm length, 28.5 mm width) have the shortest skulls, although they are proportionally wider than both *Acrantophis* species.
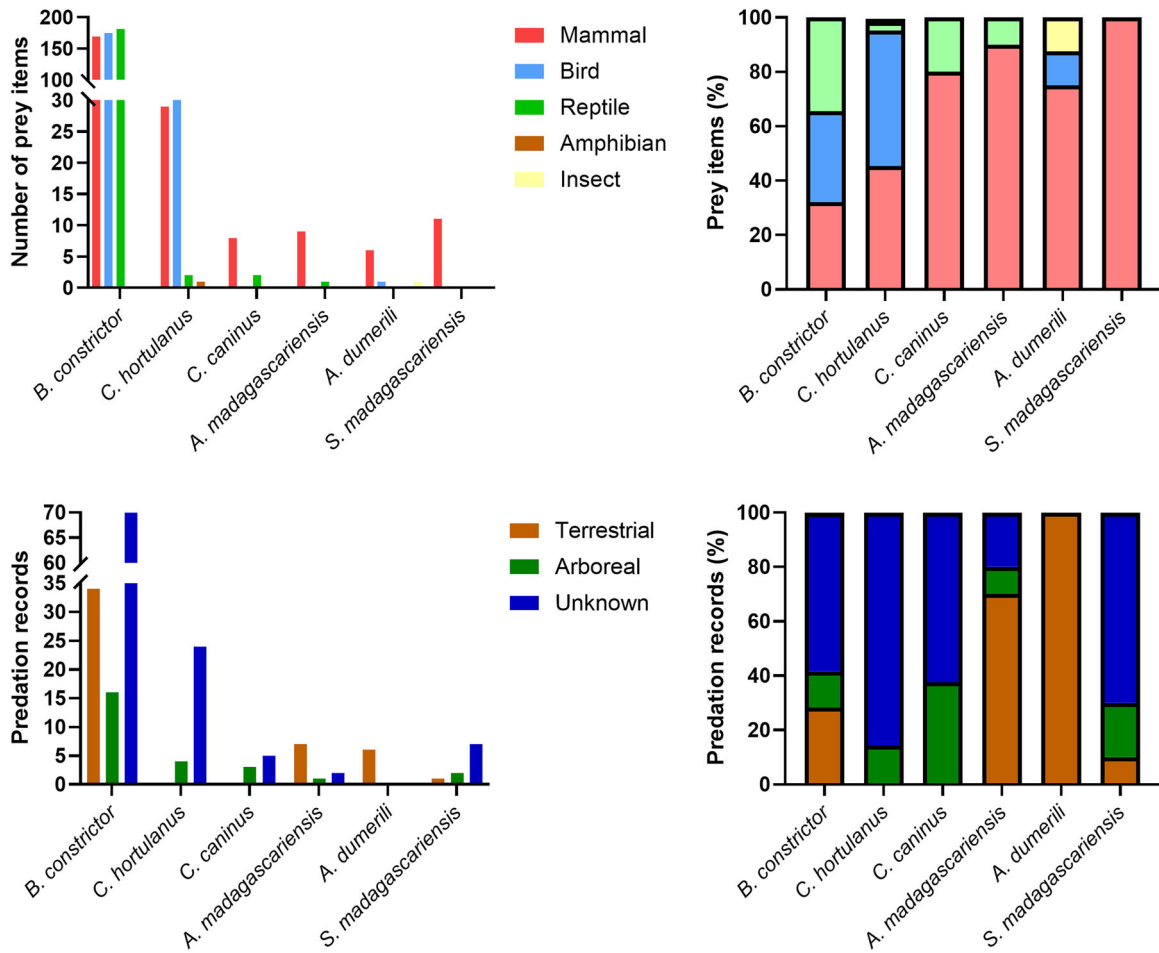

FIGURE 2 | Comparative prey proportions in the diet of select booidean snakes. *Corallus hortulanus* was included due to its position as a congener of *C. caninus* with a similarly arboreal lifestyle and a better-known diet.
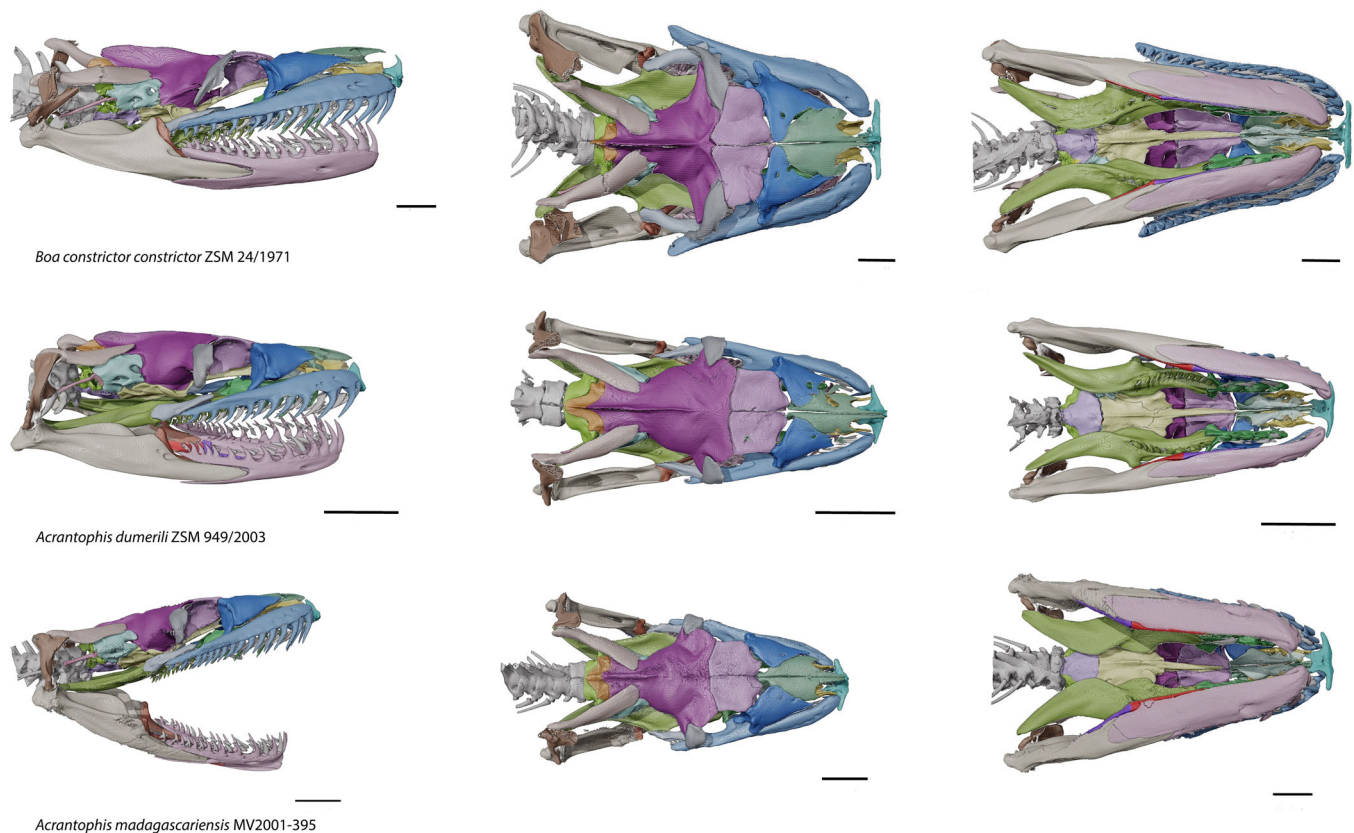
FIGURE 3 | Skulls of *Boa constrictor*, *Acrantophis dumerili*, and *A. madagascariensis* in lateral (left), dorsal (middle), and ventral (right) view. Note the streamlined, elongated head shape, proportionally short teeth, and the compound bones extending in length rather than height. Scale bars = 10 mm.

3.3 | Premaxilla (Figures 5 and 8A)

Acrantophis and *Boa* present similar premaxillae: the transverse process is broad (Figures 5 and 8A), the distal tips lying anterior to the maxilla. The *Boa* premaxilla is straight, while in *Acrantophis* the transverse process is slightly curved posterodorsally. By contrast, the premaxilla in *S. madagascariensis* is considerably smaller in size (Figure 5), being enclosed between the maxillae instead of anterior to them. Furthermore, the nasal and vomerine processes occupy a larger proportion of the posterior surface relative to *Acrantophis* and *Boa*. The two Madagascan genera present a deep ascending process, while in *Boa* the process is considerably shallower, and exceptionally thin at its dorsal tip (which is curved posterodorsally). By contrast, the bifurcated posterior portion of the vomerine process is shorter in *Boa* and *Sanzinia* (both 5% skull length) than in *A. madagascariensis* (8% skull length), which results in a narrower floor of the premaxilla compared to the latter species. In *Sanzinia*, the premaxilla does not contact any other bone directly. The transverse process appears remarkably thicker in *Acrantophis* than in *Boa*, with the nasal process contacting the nasal in both genera. *Acrantophis* presents a foramen on either side of the transverse process, which are absent in *Sanzinia*.

A midline ridge is clearly visible on the ventral surface of the vomerine process in *Sanzinia*; no similar structure was detected in the other genera. In *Boa*, the transverse process appears to overlap the vomerine process ventrally, a characteristic that was not detected in the other genera. In *Boa* and *Acrantophis*, the transverse process extends laterally to form a horizontal line, while *Sanzinia* presents a considerably shorter transverse process (Figure 5), which results in a triangular shape of the premaxilla anteriorly. The anterior surface of the ascending process is concave in *Acrantophis* and convex in *Sanzinia*. The premaxilla in *Corallus* is markedly different from that of the other genera. The ascending process is disproportionately long with a bulbous medial section, while the transverse process, which appears roughly straight as in *Boa*, is scarcely longer than in *Sanzinia* (Figure 5). The nasal process is pronounced and elongated posteriorly, while the vomerine process presents exceptionally thin and short bifurcations (~3 mm) in its posterior portion.

3.4 | Septomaxilla (Figures 6 and 8B)

The structure of the septomaxilla is roughly the same in *Boa* and *Acrantophis*, with both genera presenting a labially convex and lingually concave bone. Both the dorsolateral process and the conchal process are longer but noticeably thinner in *Boa* and *Acrantophis* than in *Sanzinia*, and curve sharply inward above the vomer in the latter. The dorsolateral process is exceptionally elongated in *Corallus*, whereas the conchal process virtually absent. The anterior portion of the bone is much longer in Boa and *Corallus* than in *Acrantophis* and *Sanzinia*; in the latter pair, it is short, with a truncated end in both *Sanzinia* species, and distinct medial and lateral processes in both *Acrantophis* species.
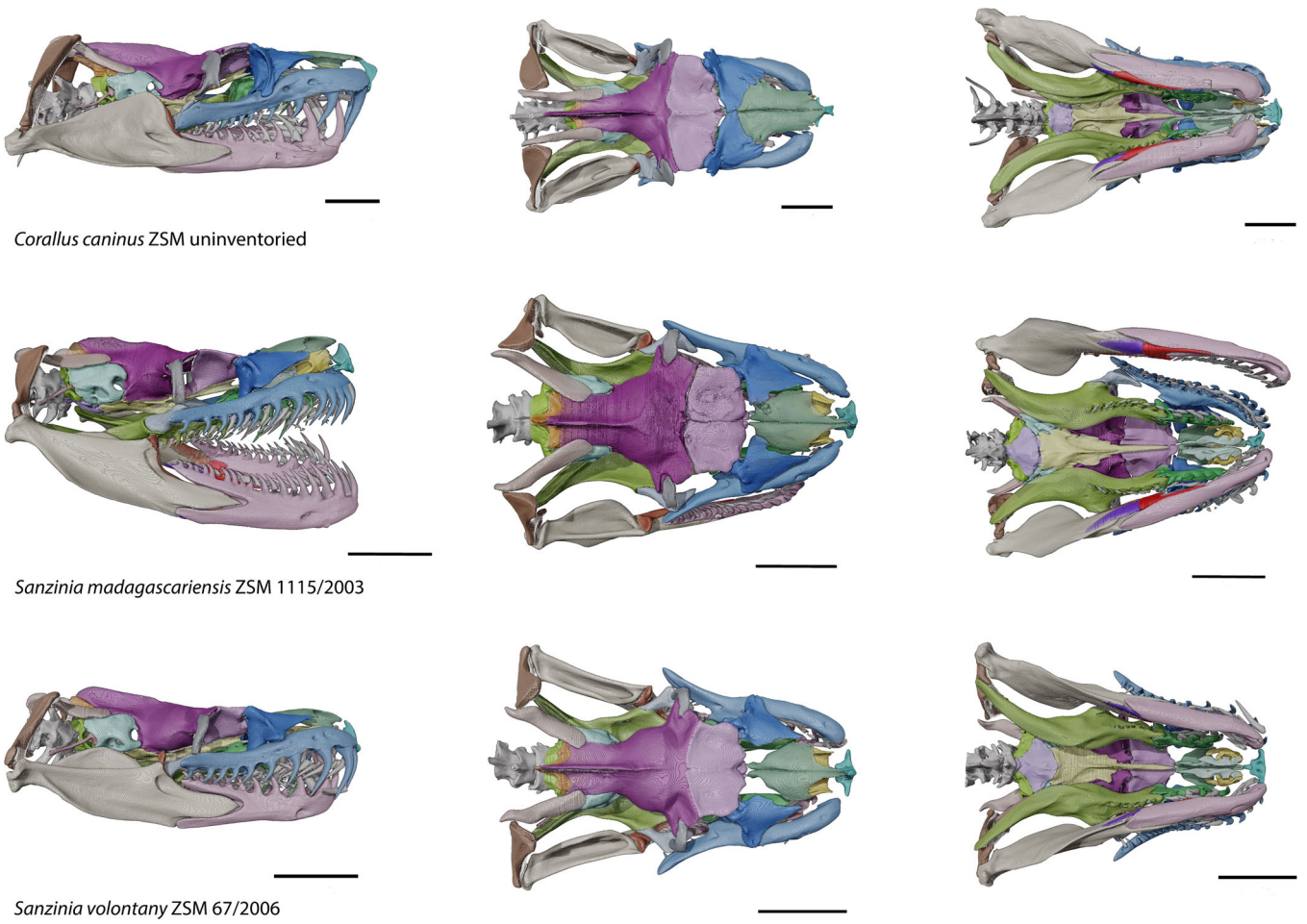
Corallus caninus ZSM uninventoried

Sanzinia madagascariensis ZSM 1115/2003

Sanzinia volontany ZSM 67/2006

FIGURE 4 | Skulls of *Corallus caninus*, *Sanzinia madagascariensis*, and *S. volontany* in lateral (left), dorsal (middle), and ventral (right) view. Note the funnel-shaped head structure tapering down toward the snout, long teeth in proportion to skull size (especially in *C. caninus*), and compound bones extending vertically as well as in length. Scale bars = 10 mm.
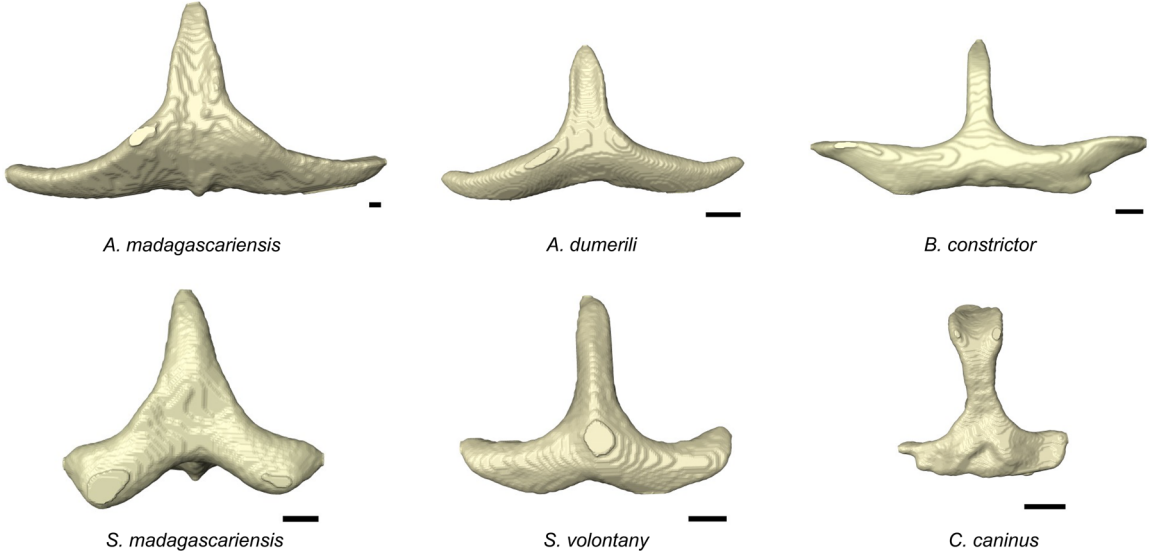

Premaxilla

A. madagascariensis

A. dumerili

B. constrictor

S. madagascariensis

S. volontany

C. caninus

FIGURE 5 | Comparison of premaxillae in anterior view. Scale bar = 1 mm.

3.5 | Vomer (Figures 7 and 8C)

The shape of the vomer is overall similar among *Sanzinia, Boa*, and *Acrantophis*, albeit with intrageneric variation. The bone is of roughly constant width along its extension in *Sanzinia*, with a slight indentation in the lateromedial section (Figure 7). The external vomeronasal fenestra is small in the Madagascan genera, but considerably larger in *Boa* (the caudal margin is nonetheless
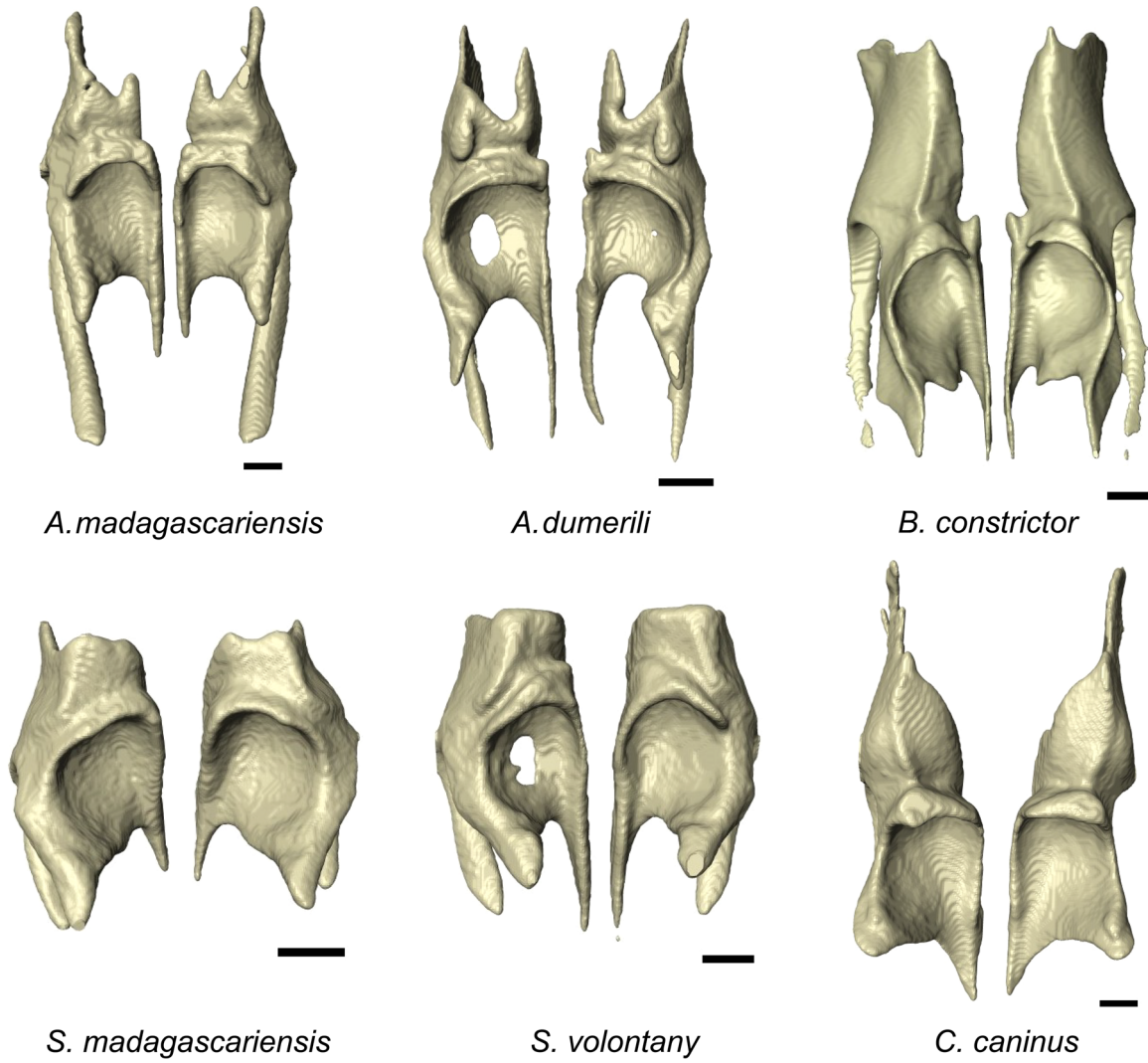
Septomaxilla

A. madagascariensis

A. dumerili

B. constrictor

S. madagascariensis

S. volontany

C. caninus

FIGURE 6 | Comparison of septomaxillae in ventral view, with anterior end at top. Scale bar = 1 mm.

Vomer

A. madagascariensis

A. dumerili

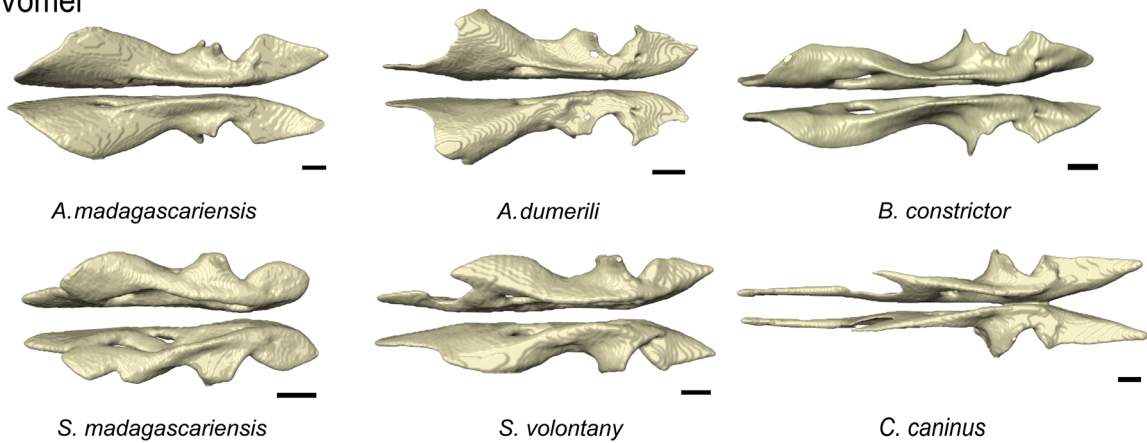B. constrictor

S. madagascariensis

S. volontany

C. caninus

FIGURE 7 | Comparison of vomers in dorsal view, with anterior end at right. Scale bar = 1 mm.

directed anterolaterally in all the four genera). Furthermore, *Boa* presents a clear difference between the anterior and posterior section of the horizontal lamina, the former consisting of two wide anterolateral processes that terminate in two elongated, acuminate medial appendages, while the latter is considerably narrower and presents two slightly convex posterolateral processes (Figure 8C). The vomer of *Corallus* differs from that of the other genera. In *Corallus*, the posterior section of the horizontal
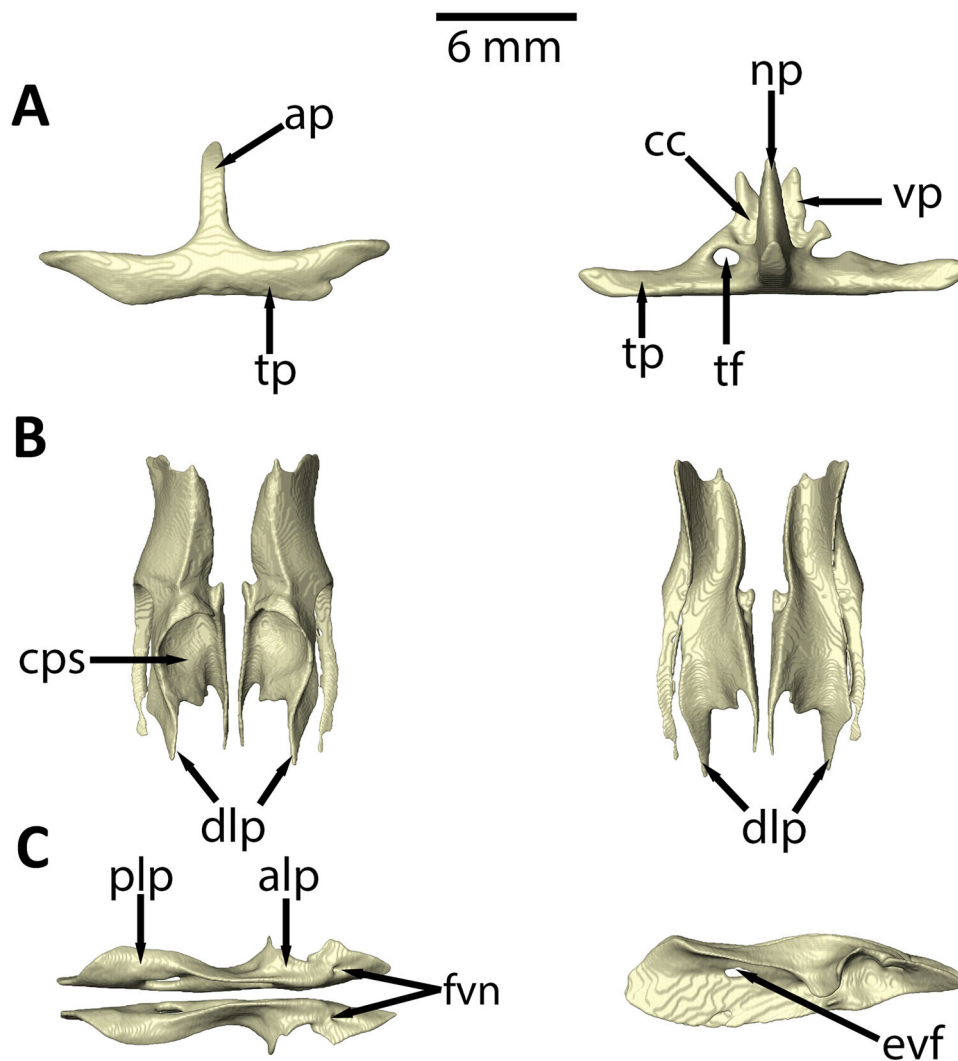
FIGURE 8 | Premaxilla (A), septomaxilla (B), and vomer (C) of *Boa constrictor*. (A) Premaxilla in frontal (left) and dorsal (right) view. (B) septomaxilla in dorsal (left) and ventral (right) view. (C) Vomer in dorsal (left) and lateral (right) view. alp = anterolateral process, ap = ascending process, cps = conchal process, dlp = dorsolateral process, evf = external vomeronasal fenestra, fvn = vomerine foramen for vomeronasal nerve, np = nasal process, plp = posterolateral process, tf = trigeminal foramen, tp = transverse process, vp = vomerine process.

lamina is narrow and presents no processes, while the medial and anterior sections are considerably wider (Figure 7). Finally, in *Acrantophis* the two posterolateral processes are wider than their anterolateral counterparts, and two more processes, albeit short, are visible lateromedially (Figure 7). Common to all four genera is a distinct midline ridge.

3.6 | Nasal (Figures 9 and 11A)

In *Sanzinia*, the anteroventral process of the nasal is considerably shorter than in *Boa*, and especially *Acrantophis*, which possesses the longest process among the three genera. Furthermore, the bone appears generally shorter in *Sanzinia* than in *Acrantophis, Corallus*, and especially *Boa* (Figure 9), with the prefrontals barely contacting it. Moreover, *Boa, Corallus*, and *Acrantophis* present a longer junction, as well as a considerably thinner posterior section of the horizontal lamina. The nasal does not contact the frontal in the Madagascan genera, while it does in *Boa*. Three foramina are present on the left nasal bone in

Sanzinia and *Boa*, but appear to be absent in *Acrantophis* (Figures 9 and 11A). The nasal is far more raised in *Sanzinia* than in *Boa, Corallus*, and *Acrantophis*, abruptly curving upward and thus breaking the skull line. Readily noticeable indentations at the anterior and anterolateral margins of the ventral lamina are common to *Boa, Acrantophis*, and *Sanzinia. Corallus* presents a different conformation of the nasal: the bone is remarkably linear, with exceptionally short anteroventral processes and complete lack of indentations (Figure 9). The nasals are encased between the prefrontals posteriorly, and do not contact the frontals, while the premaxilla is in direct contact with them anteriorly. No foramina were observed in this genus.

3.7 | Prefrontal (Figures 10 and 11B)

The prefrontal bone is similar in *Boa* and *Acrantophis*, but the former presents a longer and more discernibly concave bone at the junction with the nasal (Figure 10). Furthermore, in *Boa* the two prefrontals are almost in contact (Figure 11B), thereby preventing
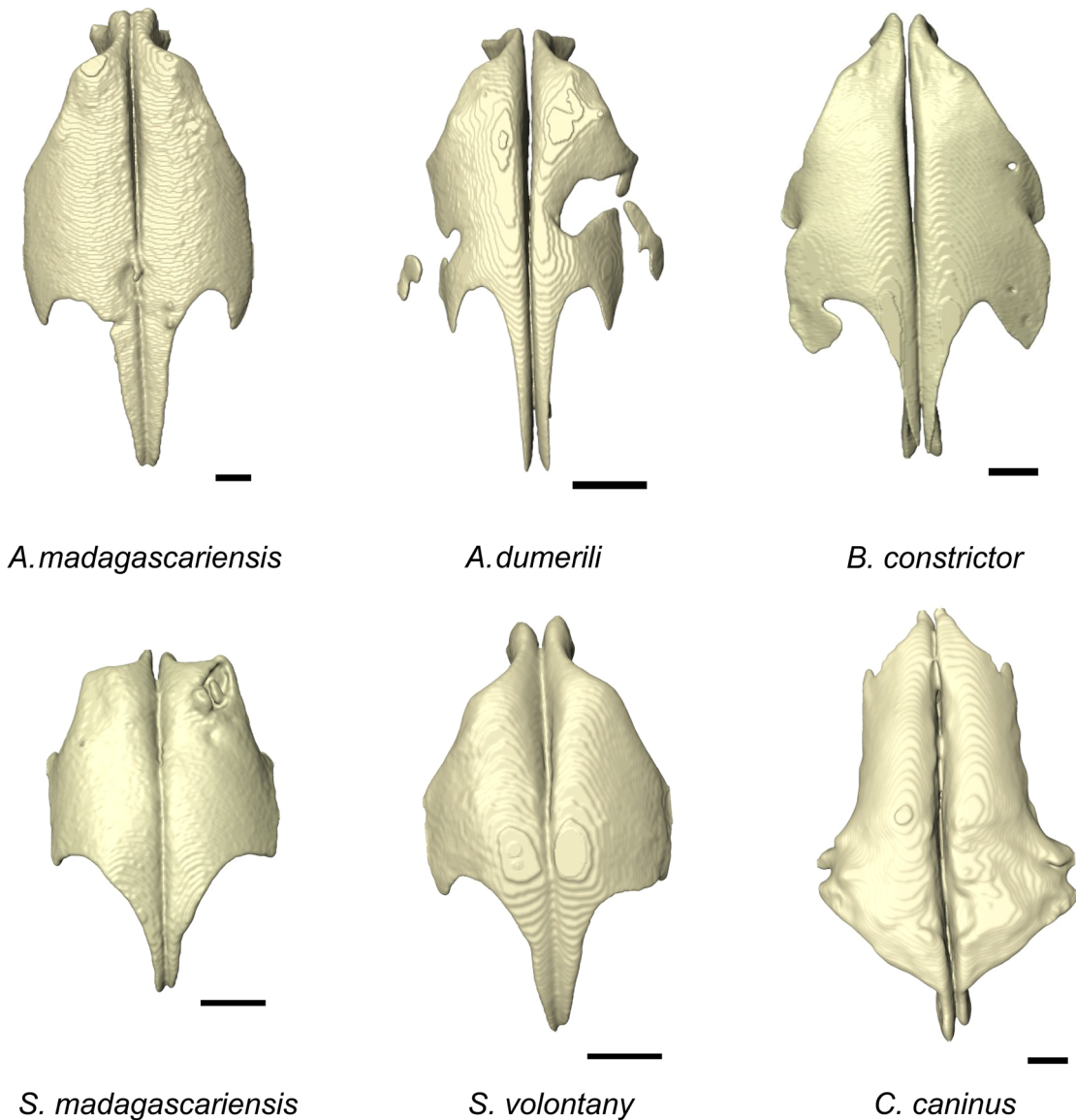
FIGURE 9 | Comparison of nasals in dorsal view, with anterior end at top. Scale bar = 2 mm.

any contact between the nasals and the parietal in dorsal view. *Sanzinia* has a shorter and wider prefrontal bone in proportion to skull length, and the two foramina (Figure 11B) are shifted posteriorly with respect to *Boa* and *Acrantophis*, which present them anteromedially (Figure 10). The foramina in *Sanzinia* are considerably smaller than in the other two genera. Common to all three genera is the short extension of the lateral foot process, which does not extend over the maxilla but only overlaps it partially.

In lateral view, the prefrontal appears roughly triangular, with a sharp angle formed by the lateral foot process and the lateroventral margin of the horizontal lamina. However, *Corallus* presents a remarkably elongated lateral foot process, which does not extend over the maxilla but appears more pronounced than in the other three genera (Figure 10). Furthermore, its prefrontals contact each other, separating the nasals from the frontals, and the foramina are positioned posteriorly as in *Sanzinia*. Both the anterior and posterior margins of the prefrontals are irregular and slightly indented in *Corallus* (Figure 10). The

prefrontal is roughly at a right angle to the axis of the skull in all species but *B. constrictor* and *S. madagascariensis*, which present slightly anteriorly angled prefrontals. However, this might be due to damage to the skull structure. Common to all species is the anterolateral orientation of the bone.

3.8 | Frontal (Figures 12 and 15A)

In *Acrantophis*, the frontal appears more raised with respect to the prefrontal than in *Boa*, *Corallus*, and *Sanzinia*, which present it on the same level, so that it is hardly visible in anterior view of the articulated skull. The frontals of *Sanzinia*, *Boa*, and *Acrantophis* are almost identical, appearing compact and roughly linear, although the bone narrows down posterolaterally in a V-shape in *Boa* and *Acrantophis* only (Figures 12 and 15A). In *Corallus*, the frontal is distinctly wider than long, resulting in a peculiar wing-like appearance (Figure 12). The frontal of the two Neotropical genera contacts the prefrontal
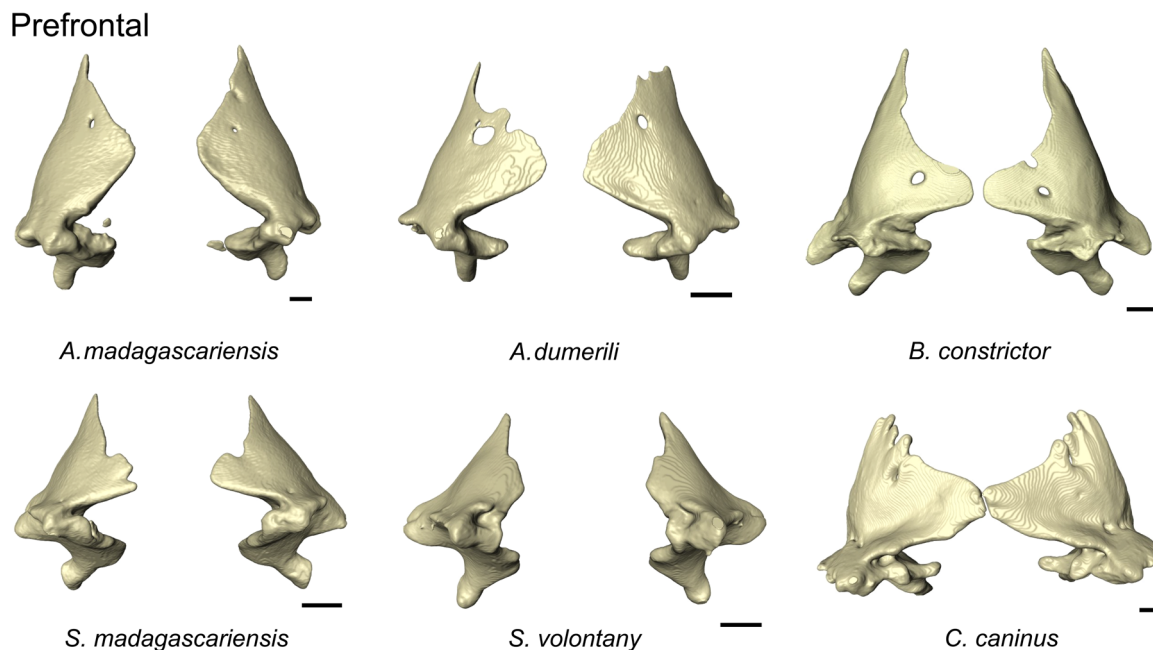
Prefrontal

A.madagascariensis   *A.dumerili*   *B. constrictor*

S. madagascariensis   *S. volontany*   *C. caninus*

FIGURE 10 | Comparison of prefrontals in dorsal view, with anterior end at top. Scale bar = 2 mm.
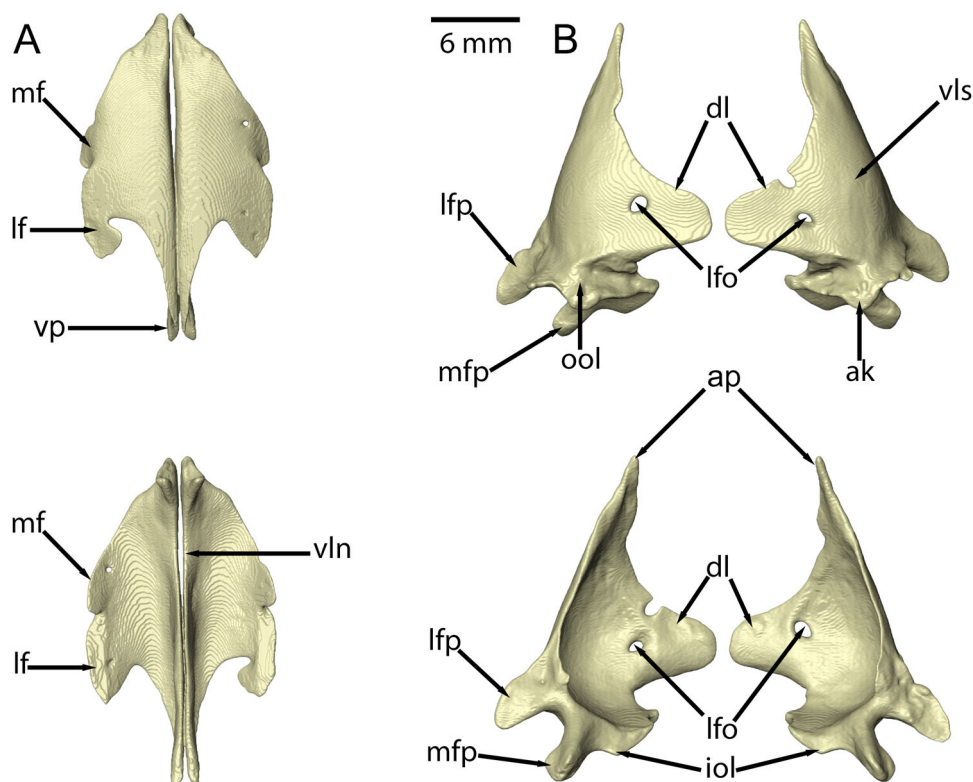

FIGURE 11 | Nasals (A) and prefrontals (B) of *Boa constrictor* in dorsal (top) and ventral (bottom) view. ak = articular knob, ap = ascending process, dl = dorsal lappet, iol = inner orbital lobe, lf = lateral flange, lfo = lacrimal foramen, lfp = lateral foot process, mf = medial flange, mfp = medial foot process, ool = outer orbital lobe, vln = ventral lamina of nasal, vls = ventrolateral shelf, vp = vomerine process.

along most of its anterior margin, while in *Acrantophis* the junction site represents only a small fraction of the bone's anterior rim. Unlike the other genera, the frontal bone is not in contact with the nasal in *Sanzinia*. In *Boa*, the frontal directly contacts the vomer anteriorly on the ventral side.

3.9 | Postorbital (Figures 13 and 15B)

In *Acrantophis*, the postorbital presents a slight concavity on the ventral side and appears almost vertical in anterior view. The overall shape of the postorbital is identical in *Boa* and *Corallus* as well,
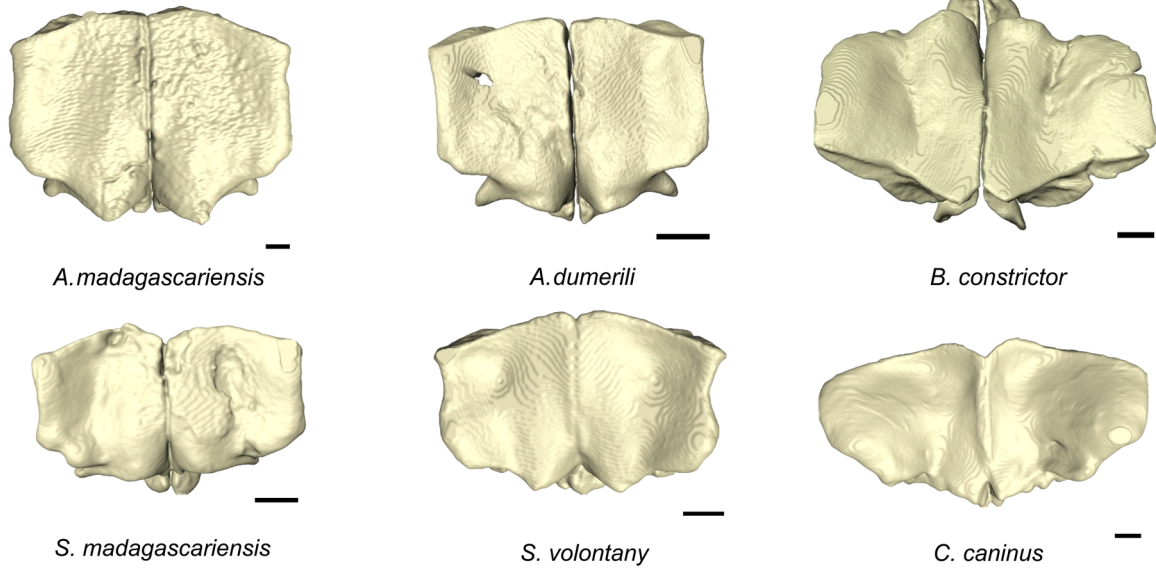
Frontal

FIGURE 12 | Comparison of frontals in dorsal view, with anterior end at top. Scale bar = 2 mm.
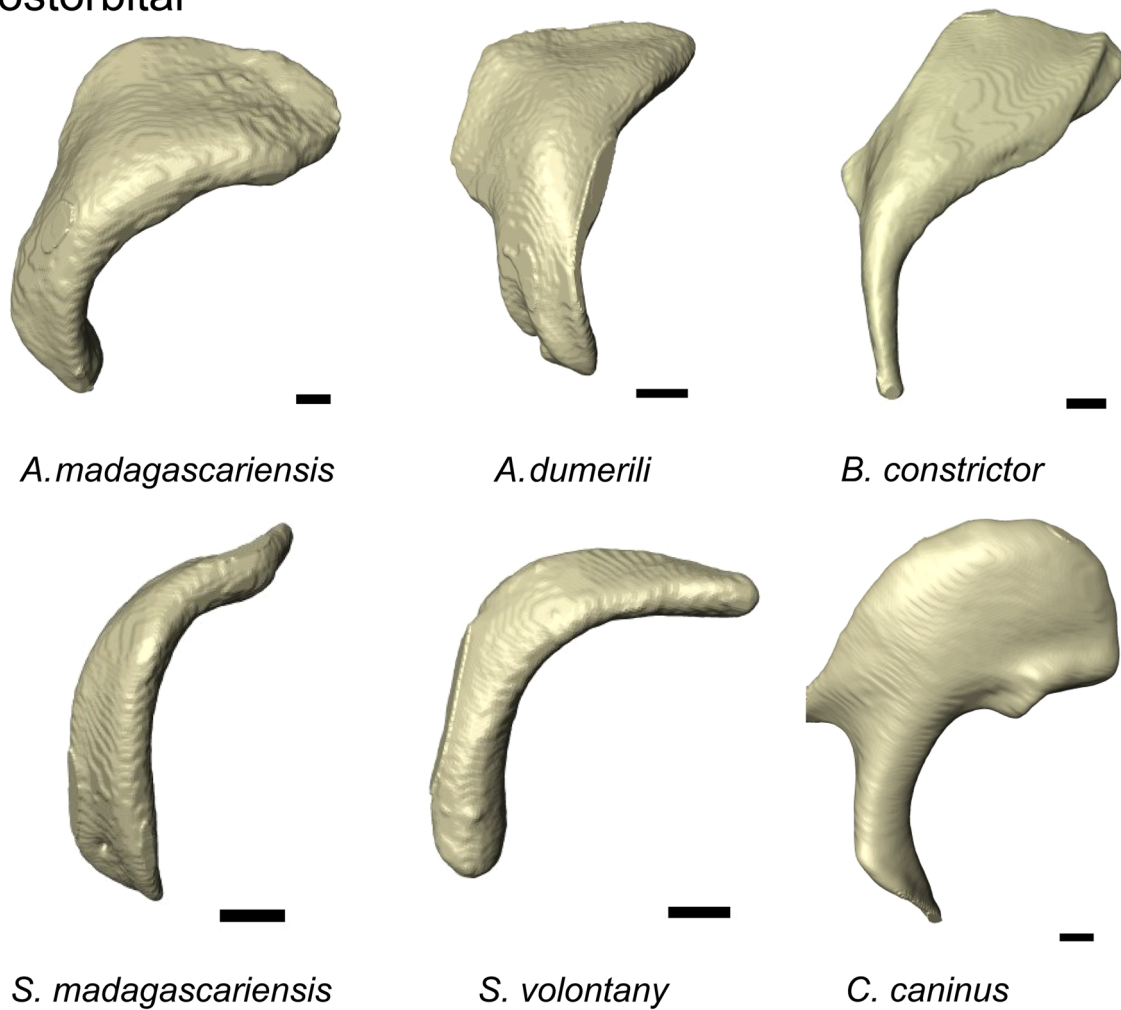
Postorbital

FIGURE 13 | Comparison of left postorbitals in lateral view, with anterior end at left. Scale bar = 1 mm.
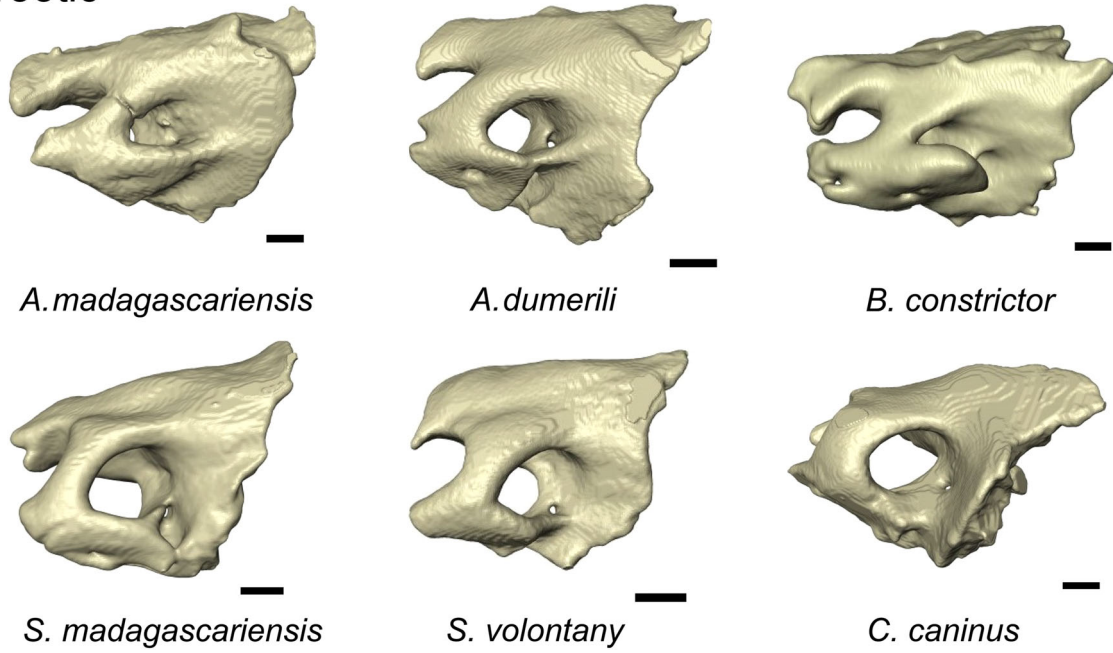
Prootic

FIGURE 14 | Comparison of prootics in lateral view. Scale bar = 1 mm.
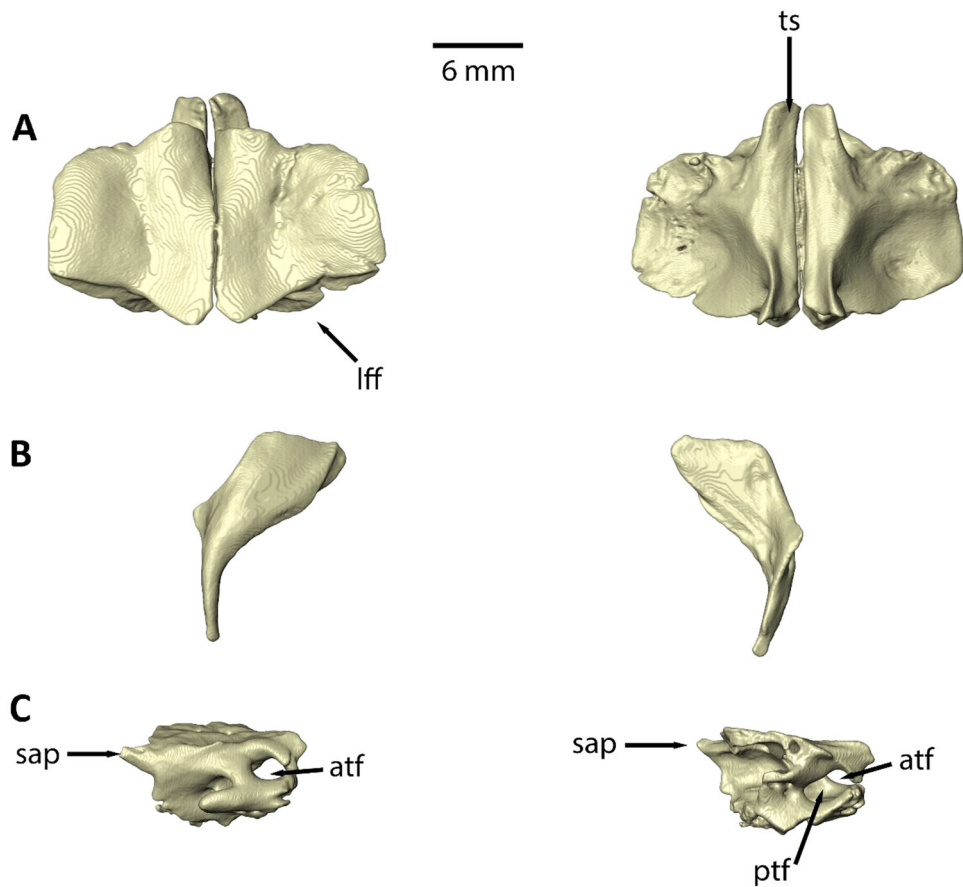

FIGURE 15 | Frontal (A), postorbital (B), and prootic (C) of *Boa constrictor*. (A) Frontal in dorsal (left) and ventral (right) view. (B) Postorbital and (C) prootic of in outer (left) and inner (right) view. atf = anterior trigeminal foramen, lff = lateral front flange, ptf = posterior trigeminal foramen, sap = superior alar process, ts = transverse shelf.

whereas the bone is distinctly narrower and thinner in *Sanzinia* (Figure 13). However, the postorbital in *Boa* and *Corallus* is remarkably thin and shifted posteriorly (narrowing progressively while extending downward) but also distinctly convex laterally, extending considerably further away from the optical cavity compared to the Madagascan genera (Figures 13 and 15B). Nonetheless, the postorbital is considerably wider in *Corallus* in proportion to skull length. Furthermore, the bone bifurcates ventrally into two processes (a shorter ventral one and a longer posteroventral one), which are absent in *Boa* and the Madagascan species.

3.10 | Prootic and Laterosphenoid (Figures 14 and 15C)

The structure of the prootic is roughly uniform in *Boa, Corallus, Sanzinia,* and *Acrantophis,* with only minor differences. In the Madagascan genera the laterosphenoid—described as a separate bone by Genest-Villard (1966)—extends from the medial section of the prootic, whereas it is shifted slightly anteriorly in *Boa* and is thicker in *Corallus* (Figure 14). *Sanzinia* presents proportionally larger foramina than *Boa* and *Acrantophis,* but those of *Corallus* are larger still (Figure 14).

3.11 | Parietal (Figures 16 and 18A)

In *Boa,* the parietal is exceptionally narrow medially, with a wider, bulbous dorsolateral region (common to all other genera as well) and a clearly visible sagittal crest (Figures 16 and 18A). Furthermore, the parietal is noticeably concave anteriorly at the junction with the frontal, which "intrudes" into it. The bone is especially narrow posteriorly, where it barely separates the two supratemporals. The parietal of *Corallus* is similar in shape, albeit with a proportionally longer ridge that extends further posteriorly (Figure 16). In *Acrantophis* and *Sanzinia,* the parietal is far wider medially and no anterior concavity is observed (Figure 16). Finally, the midsagittal crest is more pronounced in *Boa, Corallus,* and *Sanzinia* than in *Acrantophis,* although *Sanzinia*'s crest is shorter in length.

3.12 | Basisphenoid (Figures 17 and 18B)

In *Boa,* the basisphenoid is considerably smaller than in *Acrantophis* and *Sanzinia* in proportion to skull size (Figure 17). The shape of the bone resembles a spearhead, with a linear posterior end that extends anterolaterally to form the parasphenoid wings. The vidian canals appear of identical size, albeit extremely small and barely visible. This results in a wide medial section, which shrinks again anteriorly at the posterior end of the parasphenoid process (Figures 17 and 18B). *Corallus* presents a similar conformation in the vidian canals, but the parasphenoid wings are more pronounced, extending laterally to be overlapped by the pterygoid. In the Madagascan snakes, the bone is more compact, with the posterior end being slightly concave and the medial section barely wider (Figure 17). *Acrantophis* presents a pattern more similar to that found in *Boa*: the bone narrows anteriorly to
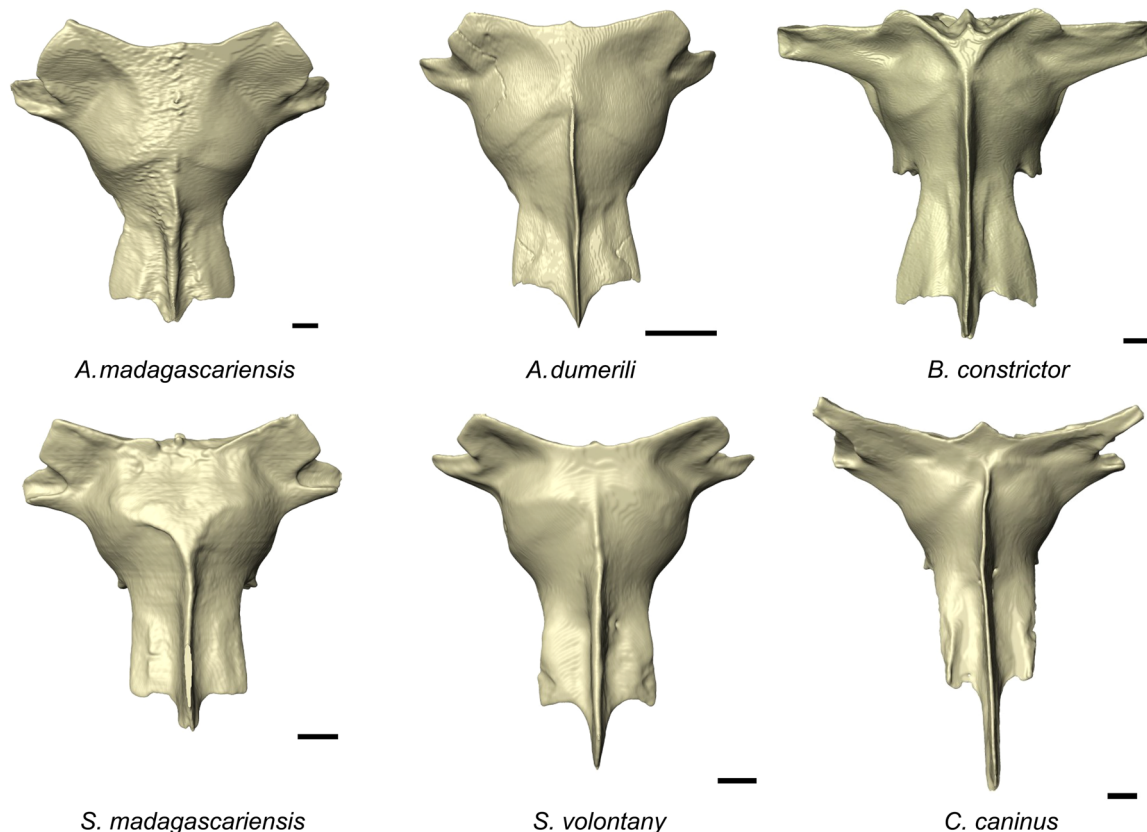
Parietal

FIGURE 16 | Comparison of parietals in dorsal view, with anterior end at top. Scale bar = 2 mm.
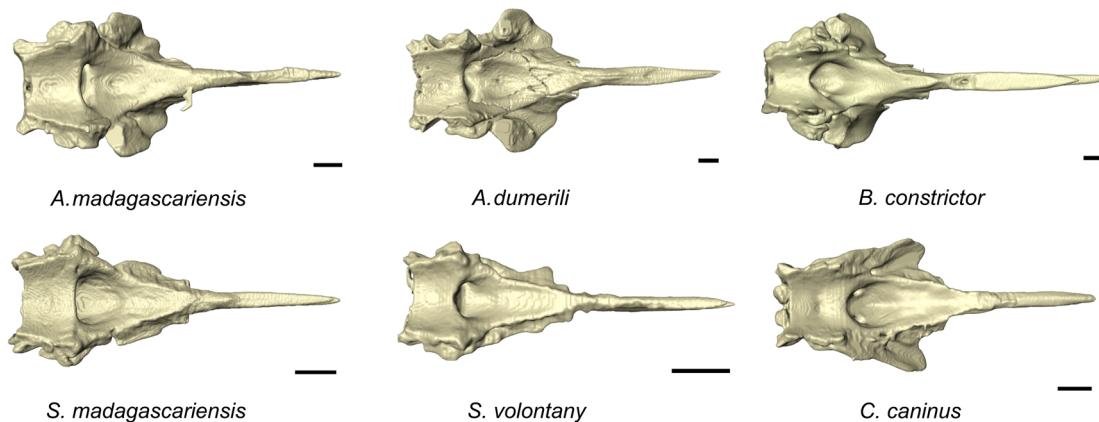
Basisphenoid

FIGURE 17 | Comparison of basisphenoids in ventral view, with anterior end at right. Scale bar = 2 mm.
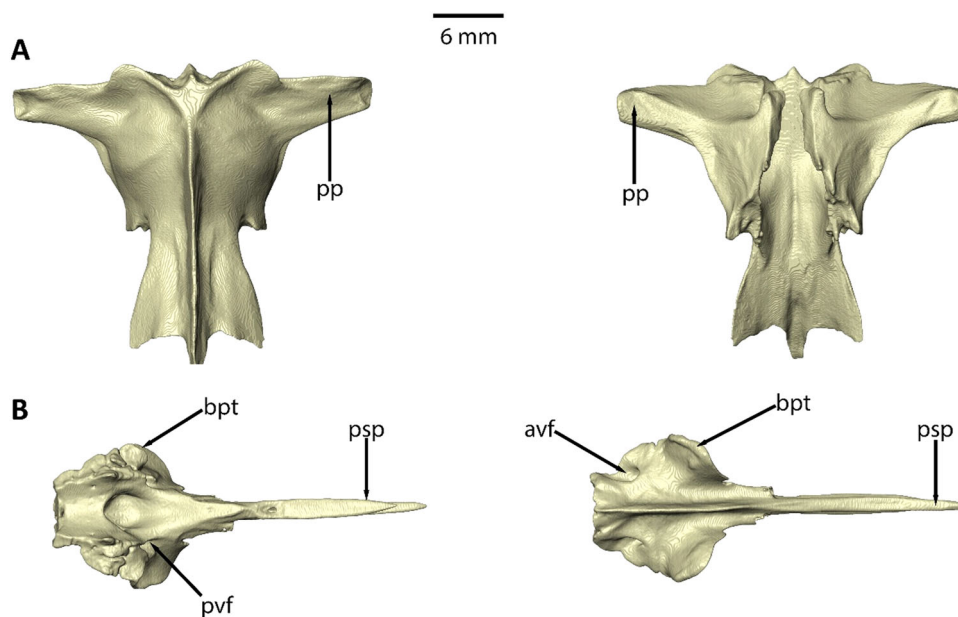

FIGURE 18 | Parietal (A) and basisphenoid (B) of *Boa constrictor*. (A) Parietal in dorsal view (left) and ventral view (right). (B) Basisphenoid in ventral view (left) and dorsal view (right). avf = anterior Vidian foramen, bpt = basipterygoid process, pp = postorbital process, psp = parasphenoid process, pvf = posterior Vidian foramina.

give rise to the parasphenoid process, with two well-developed parasphenoid wings (Figure 17); those wings are absent in *Sanzinia*. The vidian canals vary considerably in shape at the species level. All four genera present a midline ridge on the basisphenoid (keel *sensu* Kluge 1991), but in *Sanzinia* this ridge is considerably shorter than in *Boa* and *Acrantophis*.

3.13 | Parasphenoid Process of the Basisphenoid (Figures 17 and 18B)

Overall, *Sanzinia* and *Acrantophis* present similar parasphenoid processes in width and length, whereas the process appears proportionally shorter in *Corallus* (Figure 17). The parasphenoid process of *Sanzinia* does not contact the vomer, instead terminating at the anteromedial section of the frontal. In *Boa*, the parasphenoid process is remarkably deep and long,

extending from the posterior end of the basisphenoid to that of the vomer, while in *Acrantophis* and *Sanzinia* the bone is only detectable from the anterior end of the basisphenoid.

3.14 | Exoccipital (Figures 19 and 20)

Acrantophis madagascariensis presents the largest exoccipital among the analyzed species, encasing the supraoccipital in the entirety of its extension. This is not the case in *Boa*, where the exoccipital appears completely overlapped by the supraoccipital medially. However, the latter presents a wider exoccipital (Figure 19). *Sanzinia* presents a wide exoccipital laterally as well, but the medial section is completely overlapped by the supraoccipital as in *Boa*. Furthermore, the two Madagascan genera show a nearly identical conformation on the ventral side of the bone, which encases the basioccipital lateroventrally.
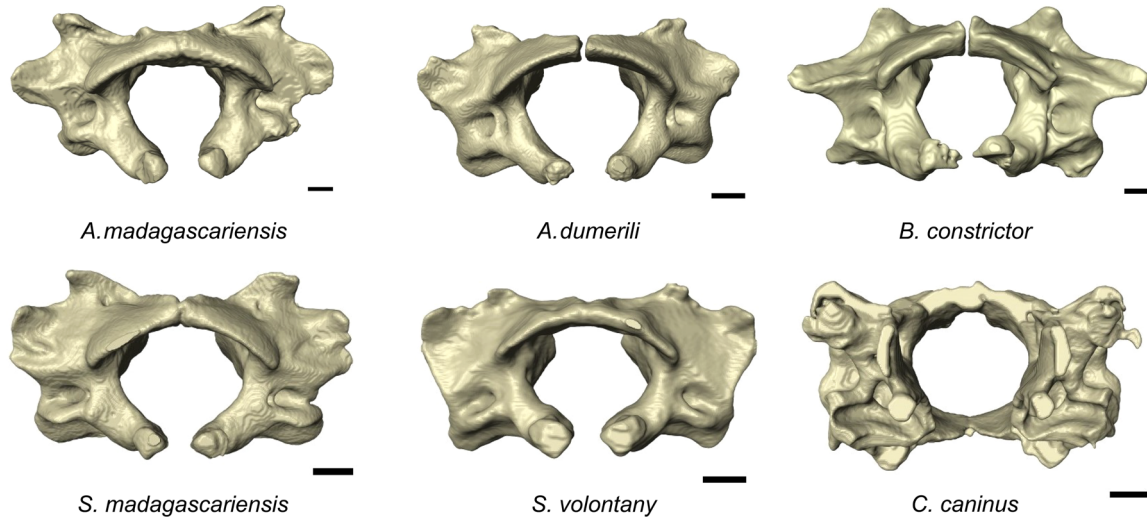
Exoccipital

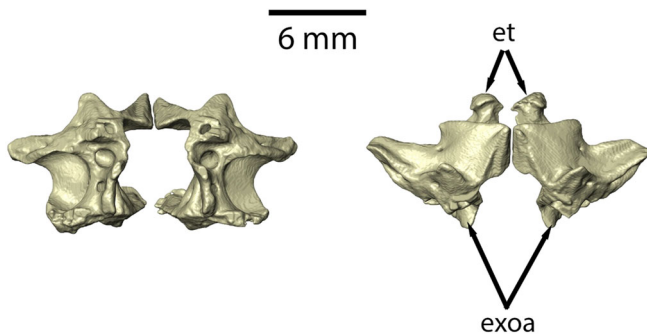**FIGURE 19** | Comparison of exoccipitals in posterior view. Scale bar = 1 mm.

FIGURE 20 | Exoccipital of *Boa constrictor* in frontal (left) and dorsal (right) view. et = exoccipital tubercule, exoa = exoccipital articular surface with supraoccipital.

This is not the case in *Boa*, where the exoccipital appears shifted posteriorly and only contacts the extreme ventral portion of the basioccipital. In *Corallus*, the exoccipital encases the supraoccipital throughout its entire lateral extension as in *Acrantophis*, and the same was observed in ventral view with respect to the basioccipital. Interestingly, the parietal sagittal crest extends all the way through the exoccipital in *Corallus*.

3.15 | Supratemporal (Figures 21 and 24A)

Boa and *Acrantophis* present similar supratemporal bones, which nonetheless are relatively longer in the latter in proportion to total skull length (Figure 21). In *Sanzinia*, the general shape of the bone is similar, but the parietal-supratemporal junction is located more posteriorly with respect to *Boa* and *Acrantophis*. The supratemporal appears more raised in *Acrantophis* and (especially) *Sanzinia* than in *Boa*. In *Corallus* and *Sanzinia*, the supratemporal is short in proportion to skull length (Figure 21), but more heavily shifted posteriorly and extending well over the quadrate, which is encased dorsally by its pronounced concavity. Furthermore, the bone is uniform in *Corallus* as opposed to wider posteriorly

as in all other genera (Figure 21). In all species, the supratemporals diverge posterolaterally.

3.16 | Basioccipital (Figures 22 and 24B)

The shape of the basioccipital is very similar in the examined Neotropical and Madagascan booideans, with a fan-like appearance tapering down posteriorly (Figure 22). The only exception is *Boa* where the basioccipital presents several appendages that are absent in the other genera (Figure 24B). Moreover, the bone is also partially overlapped by the basisphenoid anteriorly, a feature that is absent in the Madagascan genera and in *Corallus*. *Sanzinia* presents a noticeable difference in the position of the bone, which appears shifted posterodorsally (looking almost vertical) in comparison to *Boa* and *Acrantophis*.

3.17 | Supraoccipital (Figures 23 and 24C)

Among the analyzed genera, *Boa* and *Corallus* have the smallest supraoccipital bone compared to total skull length (Figure 23), although the lateral wings are wider than in the Madagascan genera. By contrast, *Sanzinia* and *Acrantophis* show a considerably longer bone in proportion, although shorter (Figure 23). A common trait between *Sanzinia* and *Boa* is the remarkably long medial section, which extends posteriorly to completely overlap the exoccipital. This is not the case in *Acrantophis* and *Corallus* despite the latter's exceptionally long sagittal crest (which is virtually absent in *A. madagascariensis* and stunted in *A. dumerili*).

3.18 | Maxilla (Figures 25 and 27A)

Acrantophis and *Boa* present similar maxillae, all narrow and elongated. However, the *Boa* maxilla appears to extend further posteriorly than in *Acrantophis*, reaching over the anterior portion of the pterygoid. Furthermore, *Boa* presents fewer
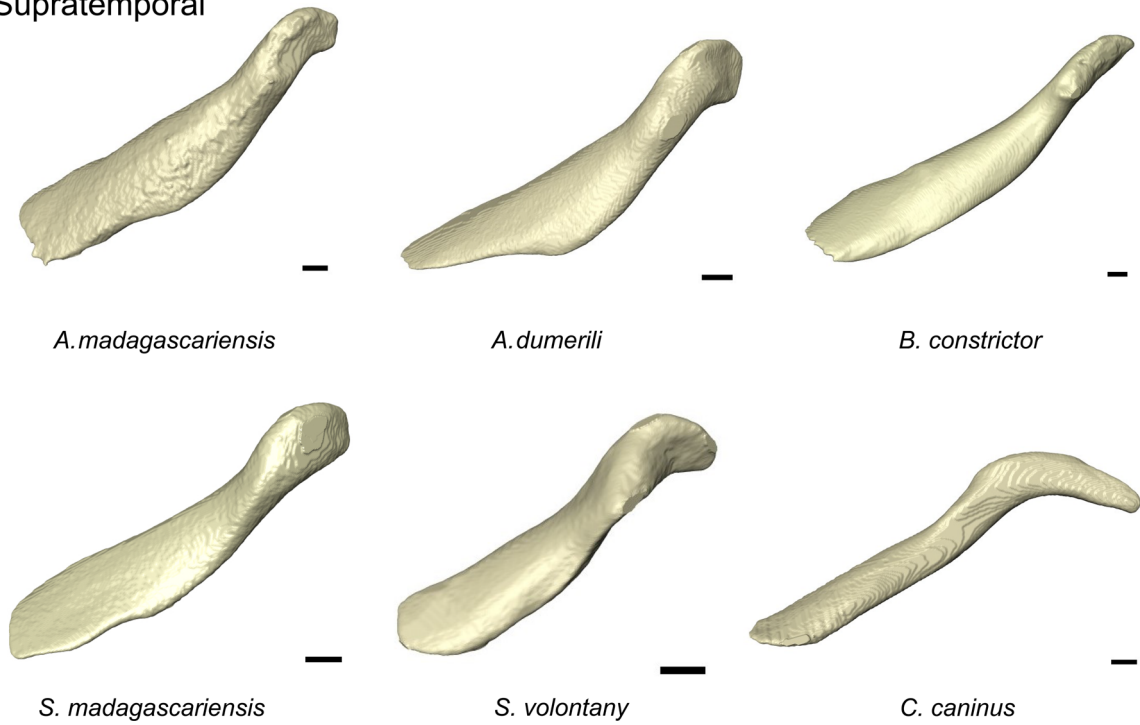
Supratemporal

FIGURE 21 | Comparison of supratemporals in dorso lateral view. Scale bar = 1 mm.
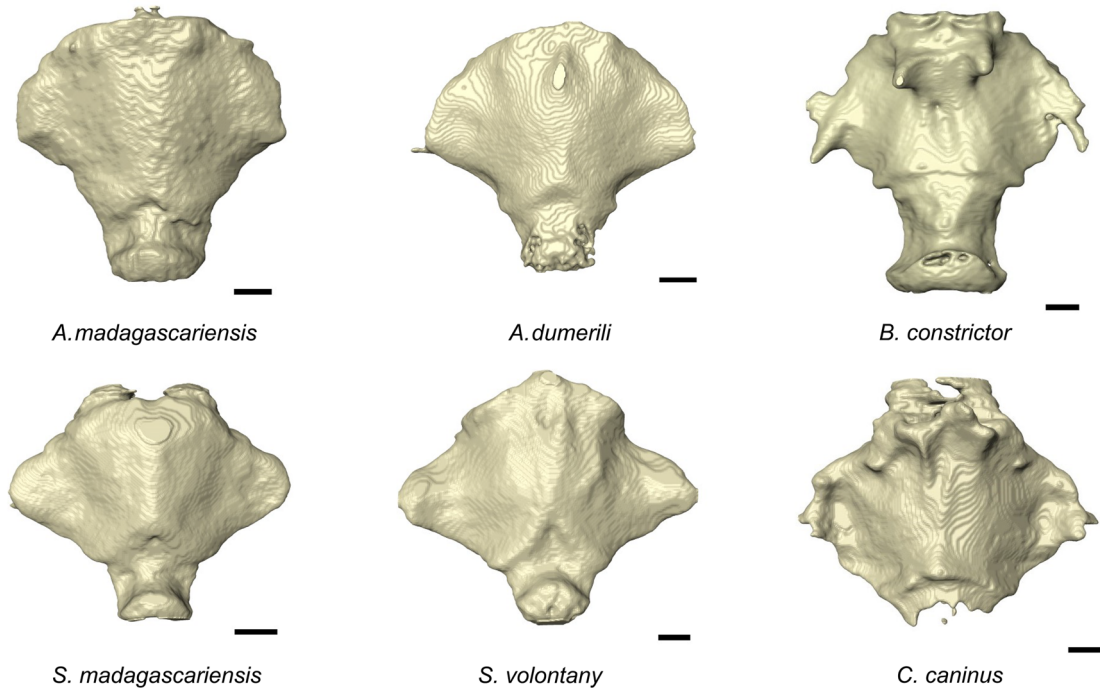
Basioccipital

FIGURE 22 | Comparison of basioccipitals in ventral view, with anterior at top. Scale bar = 1 mm.

maxillary teeth compared to *Acrantophis* (16 per row vs. 20 [number of teeth in each row on the maxilla]), but this character is likely to be influenced by the loss of teeth in the analyzed specimens (Figures 25 and 27A). However, the maxilla of *Sanzinia* is comparatively shorter in relation to skull length (Figure 27), the attachment to the ectopterygoid being located at the level of the suborbital rather than at that of the parietal like in *Boa* and *Acrantophis*. *Corallus* presents a proportionally long maxilla like *Boa*, but the depth and slight curvature of the bone aligns it with *Sanzinia* (Figure 27). Likewise, the suborbital region of the maxilla appears considerably deeper in *Sanzinia* and *Corallus* than in *Boa* and *Acrantophis*. Furthermore, the maxillary teeth in *Sanzinia* are markedly curved, with each maxilla housing more of them than in the other genera.

Supraoccipital

A.madagascariensis   *A.dumerili*   *B. constrictor*

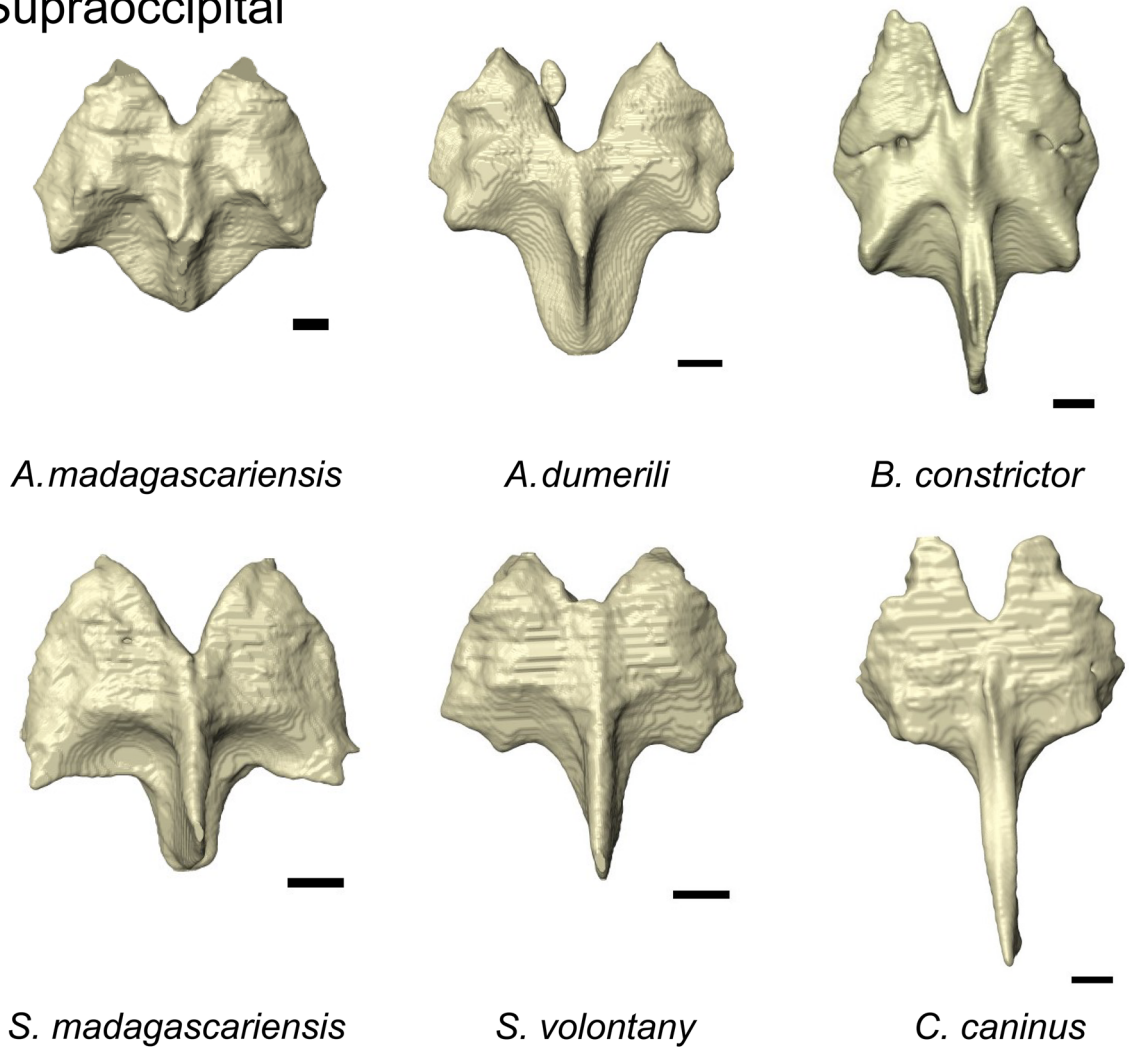*S. madagascariensis*   *S. volontany*   *C. caninus*

FIGURE 23 | Comparison of supraoccipitals in dorsal view, with anterior at top. Scale bar = 1 mm.
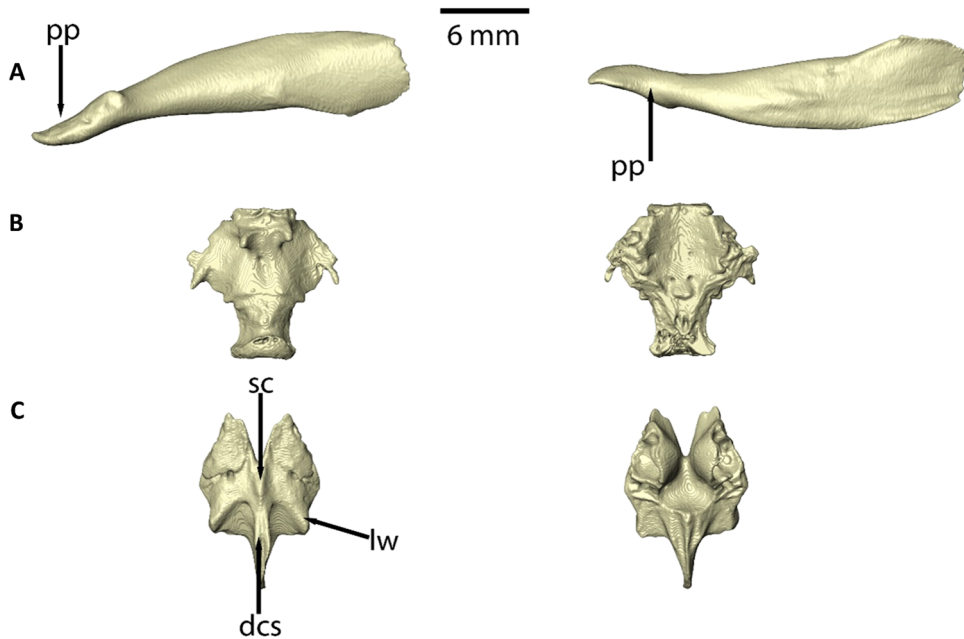

FIGURE 24 | Supratemporal (A), basioccipital (B), and supraoccipital (C) of *Boa constrictor* in dorsal (left) and ventral (right) view. dcs = dorsal crest of supraoccipital, lw = lateral wing, pp = posterior process, sc = sagittal crest.
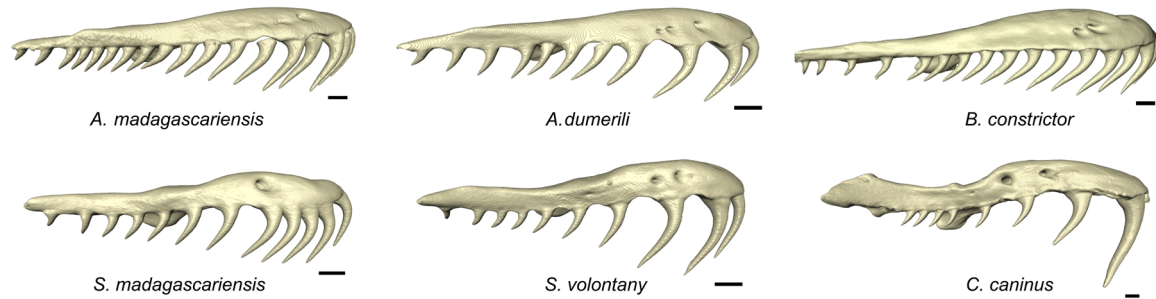
Maxilla

FIGURE 25 | Comparison of maxillae in lateral view, with anterior at right. Scale bar = 2 mm.
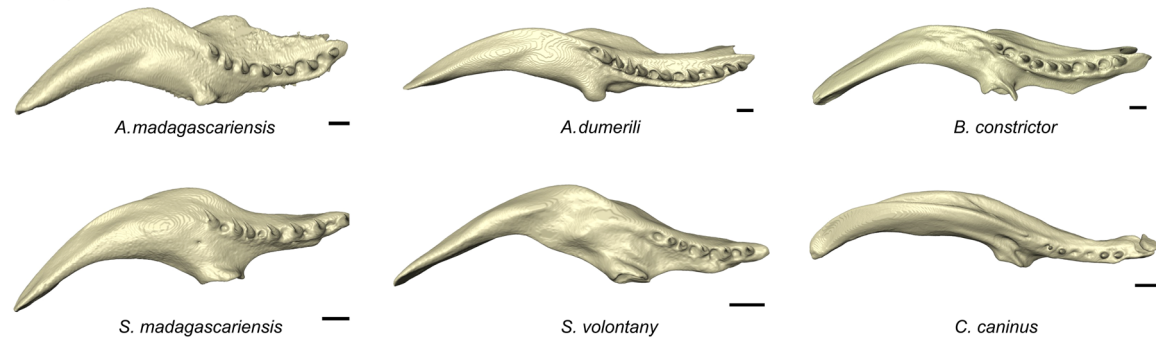
Pterygoid

FIGURE 26 | Comparison of pterygoids in ventral view, with anterior at right. Scale bar = 2 mm.
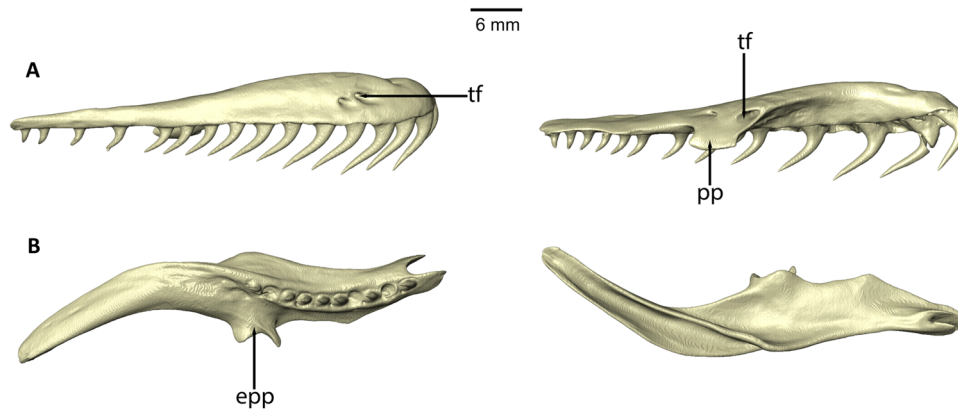

FIGURE 27 | Maxilla (A) and ptyergoid (B) of *Boa constrictor*. (A) Maxilla in outer (left) and inner (right view). (B) Pterygoid in ventral (left) and dorsal (right) view. epp = ectopterygoid process, pp = palatine process, tf = foramen for maxillary branch of trigeminal.

Sanzinia volontany has longer maxillary teeth than *S. madagascariensis* (15% vs. 11% skull length, respectively, with measurements referring to the anterior-most tooth on the maxilla). However, the longest teeth are found in *Corallus*, which presents an exceptionally large dentition anteriorly (17% skull length). However, *Corallus* has fewer maxillary teeth (12) than the other three genera. The terrestrial species all have shorter teeth in proportion to skull length (11% in *A. madagascariensis*, 10% in *A. dumerili*, and 7% in *B. constrictor*).

Boa, and especially *Sanzinia*, also have a marked posterolateral outward curve at the caudal end of the maxilla, which is less pronounced in *Corallus* and completely absent in *Acrantophis* (Figures 3 and 4). Common to *Boa*, *Sanzinia*, and *Acrantophis* is

a thin and shallow postorbital region of the maxilla, as well as a palatine process extending anteromedially at the orbit level (this process is largest in *Sanzinia*). In contrast, in *Corallus* the postorbital region is remarkably deep, showing no signs of progressive shrinking as was observed in the other three genera. Furthermore, two large foramina are present on the anterolateral surface of the maxilla in *C. caninus*.

3.19 | Pterygoid (Figures 26 and 27B)

The pterygoid is generally very similar in shape in *Boa*, *Sanzinia*, and *Acrantophis*, with the dentition ranging from the anterior end to the medial section, and the bone maintaining roughly constant

width and thickness throughout its entire extension (Figures 26 and 27B). In none of these three genera does the pterygoid directly contact the quadrate. In *Corallus*, however, the pterygoid is in direct contact with the quadrate and distinctly narrow throughout its extension (Figure 26). Moreover, the bone presents a readily noticeable concavity running throughout its posterior section in this genus.

3.20 | Palatine (Figures 28 and 30A)

In *Boa* and *Corallus*, the palatine is long and thin, with five (in *Boa*) and four teeth (in *Corallus*) arranged in a single row (Figures 28 and 30A). *Acrantophis madagascariensis* and *A. dumerili* present almost identical palatine bones, the main difference being the lack of contact between the palatine and the maxilla in the latter. The palatine teeth are remarkably large in *Boa*, being on par with the anterior maxillary teeth in terms of size, while *Corallus* presents a clearly smaller palatine dentition compared to maxillary and dentary teeth. The choanal process extends posterolaterally with a roughly rounded, irregular edge in all genera, but is exceptionally long in *Corallus*, where it is sharply curved anteriorly and extends parallel to the main body of the bone (Figure 28). The dentition is the main difference between the Neotropical and the Madagascan genera in the palatine: *Sanzinia* and *Acrantophis* present two rows of palatine teeth as opposed to the single row of *Boa* and *Corallus*, displaying a synapomorphy at the family level (Figures 3 and 4). The shape of the bone is similar, although the maxillary process is more pronounced posterolaterally in *Acrantophis* and *Sanzinia* than in *Boa* and *Corallus* (Figure 28). Nonetheless, this process lies at the level of the palatine-pterygoid joint in all species.

3.21 | Ectopterygoid (Figures 29 and 30B)

The ectopterygoid is thin and elongated in *Boa*, while *Acrantophis* has a slightly thicker and longer bone compared to total skull length (Figures 29 and 30B). *Sanzinia* and especially *Corallus* have a short, wide ectopterygoid that contacts the maxilla over a considerably shorter portion of its surface (Figure 29). In *Corallus*, the

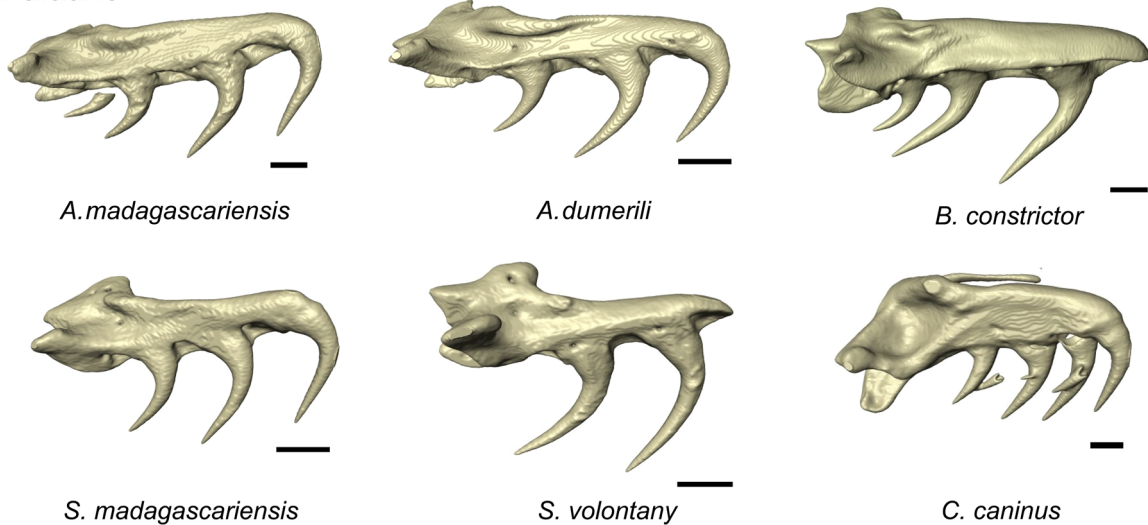**FIGURE 28** | Comparison of palatines in medial view. Scale bar = 2 mm.
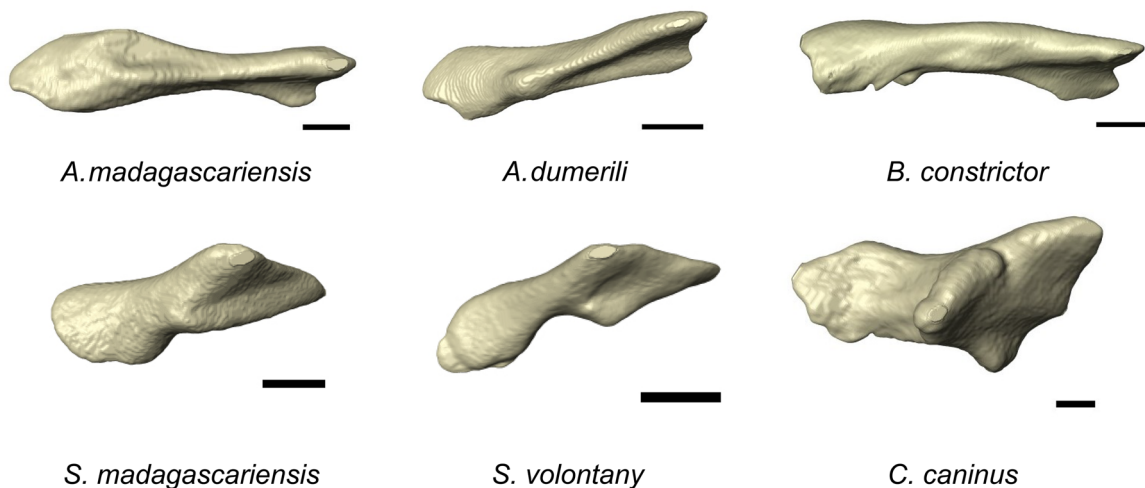

FIGURE 29 | Comparison of ectopterygoids in lateral view. Scale bar = 2 mm.

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bone appears to form two concave-convex facets that enlarge the contact surface with the maxilla, as opposed to one in all other genera. Common to the four genera is the position of the ectopterygoid-pterygoid junction, located on the lateral edge of the pterygoid and the maxilla. *Acrantophis madagascariensis* and *A. dumerili* differ in the anterior end of the bone being longer laterally in *A. madagascariensis*, overlapping the maxilla through a larger portion of its posterior end. In contrast, *A. dumerili* has a slightly thicker junction with the pterygoid posteriorly. The ectopterygoid is larger and wider anteriorly in *S. madagascariensis* than in *S. volontany*. All species have a lateral rather than dorsal junction of the ectopterygoid with the pterygoid.

3.22 | Coronoid (Figures 31 and 34A)

The coronoid is particularly elongated in *Acrantophis* and *Boa* (Figures 31 and 34A), where it is clearly discernible in

lateral and posterior view behind the coronoid process of the compound bone. In *Corallus*, the coronoid is larger than in any other genus (Figure 31) but almost completely hidden by the exceptionally tall compound bone, being barely visible even in posterior and dorsal view. The bone is proportionally wider in *Sanzinia* than in *Acrantophis* and *Boa*, with a remarkably prominent proximal end in *S. volontany* that reaches the same level as the parietal (although the two bones do not contact, and this might be influenced by the tightly closed jaws of our specimen). The coronoid contacts the splenial in all species.

3.23 | Quadrate (Figures 32 and 34B)

In *Boa*, the quadrate appears thinner than in the two Madagascan genera in proportion to length (Figure 32), with the bone presenting nonetheless a wide dorsal end at the
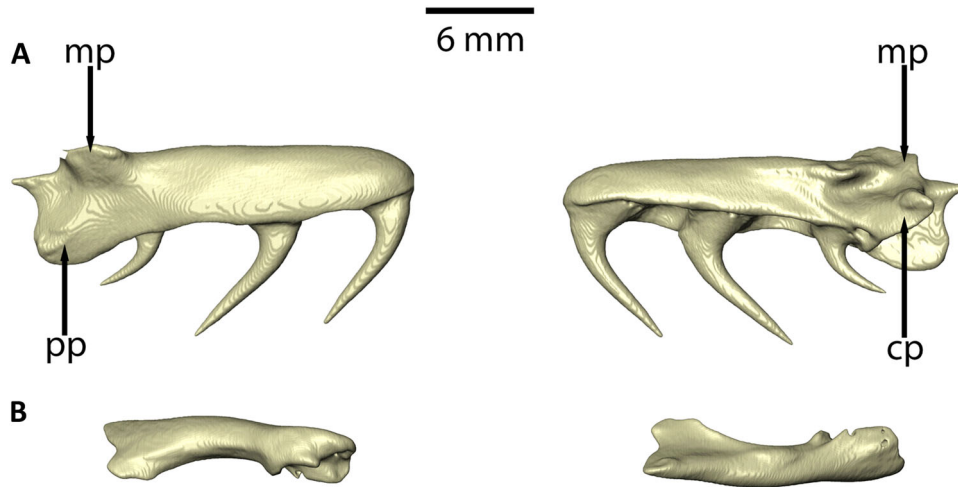

FIGURE 30 | Palatine (A) and ectopterygoid (B) of *Boa constrictor* in lateral (left) and medial (right) view. cp = choanal process, mp = maxillary process, pp = pterygoid process.
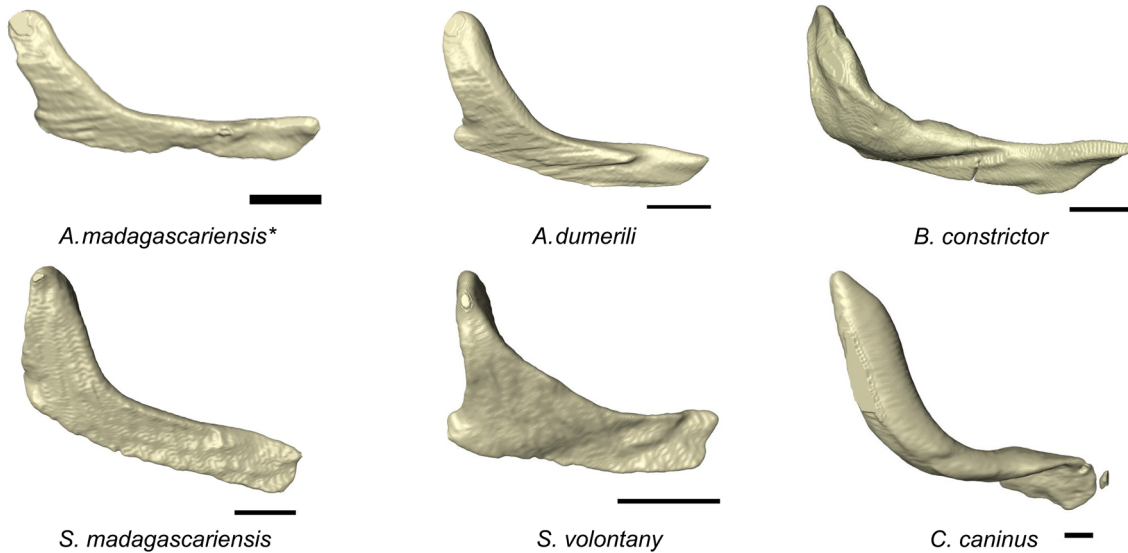

FIGURE 31 | Comparison of right coronoids in lateral view. *Left quadrate of *Acrantophis madagascariensis* shown mirrored, as the right-hand bone reconstruction had artefacts. Scale bar = 3 mm.

Quadrate

A.madagascariensis   *A.dumerili*   *B. constrictor**

S. madagascariensis   *S. volontany*   *C. caninus*
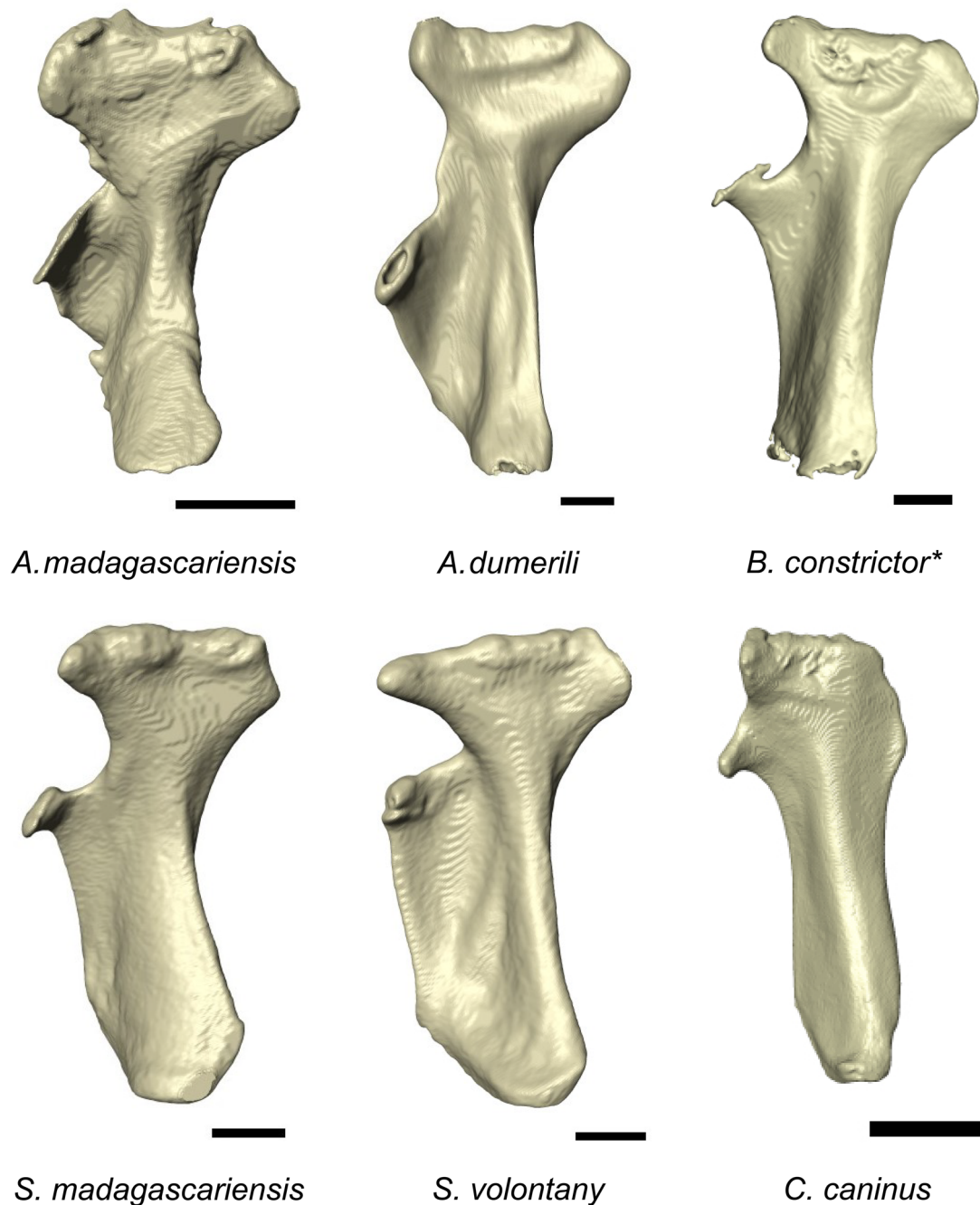
FIGURE 32 | Comparison of right quadrates in anterior view with articular surface for compound at top. *Left quadrate of *Boa constrictor* shown mirrored, as the right-hand bone was fractured. Scale bar = 2 mm.

attachment site with the supratemporal (this observation might however be biased, as the quadrate bones of our *Boa* specimen were broken at the dorsal end). This section of the quadrate is slightly convex to better accommodate the supra-temporal, while the junction with the compound bone is instead concave (Figure 34B). The same pattern can be recognized in *Acrantophis*, but the ventral end of the quadrate is narrower in this genus. *Sanzinia* presents the dorsally widest quadrate among the analyzed genera in relation to total skull length, but also the shortest (Figure 32). In none of the ana-lyzed genera does the pterygoid contact the quadrate directly.

Corallus has an exceptionally wide quadrate, with a marked concavity on the posterior side (Figure 32).

3.24 | Columella (Stapes) (Figures 33 and 34C)

In *Boa* and *Acrantophis*, the columella is horizontal and straight, looking especially thin in the former genus but longer in the latter (Figures 33 and 34C). By contrast, *Sanzinia* and *Corallus* present a uniformly short bone, which is furthermore inclined posteroventrally (Figure 33).

Columella/stapes

FIGURE 33 | Comparison of right columellae in lateral view. The left columella of *Boa constrictor* is shown because the right columella had a broekn stapedial shaft. Scale bar = 1 mm.

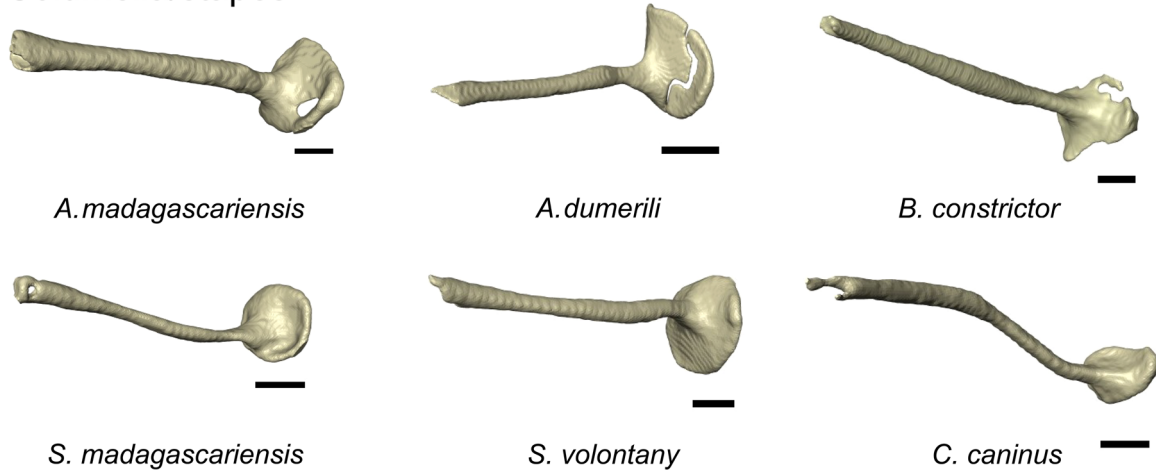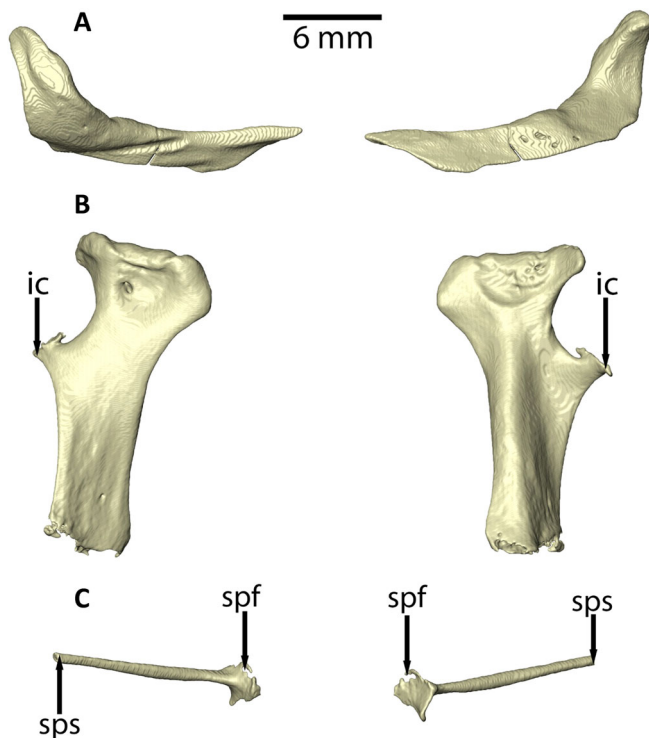**FIGURE 34** | Coronoid (A), quadrate (B), and columella/stapes (C) of *Boa constrictor* in lateral of coronoid, anterior of quadrate and columella (left) and medial of coronoid, posterior of quadrate and columella (right) view. ic = intercalary, spf = stapedial footplate, sps = stapedial shaft.

3.25 | Compound Bone (Figures 35 and 39A)

In *Boa* and *Acrantophis*, the compound bone is linear: the latter genus has short processes, with both the coronoid process and the surangular crest not protruding clearly from the main bone (Figure 35). The coronoid process constitutes the main difference between the two genera, with *Boa* presenting a considerably larger process than *Acrantophis*. *Sanzinia* differs clearly from these two genera, as it presents a taller compound bone with respect to total skull length (Figure 35). However, the muscle attachment is proportionally no wider in *Sanzinia* (~5% skull length) than in *Boa* and *Acrantophis* (~4.5–6% skull length), while the coronoid process, although more pronounced than in *Acrantophis*, is proportionately smaller than in *Boa*. The largest and deepest compound bone is found in *Corallus*: although the bone itself is the same length as in *A. madagascariensis* and shorter than in *Boa* (Figure 35), it is exceptionally tall (23.5% skull length) and wide at the muscle attachment (~8.5% skull length), with a smoothly rounded coronoid process anterodorsally (Figure 35).

3.26 | Dentary (Figures 36 and 39B)

Acrantophis and *Boa* have similar dentaries. This bone is thin and elongated in both genera, with its bifurcation being located roughly at two-thirds of its length posteriorly (Figures 36 and 39B). *Boa* has fewer teeth than *Acrantophis* (16 per row vs. 20), but the ease at which snakes lose their teeth throughout life is a heavy bias for such observations. The two Madagascan ground boas also have considerably shorter dentary teeth than *B. constrictor*, whose anterior dentition reaches 12% skull length as opposed to 8.2% in *A. madagascariensis* and 9.3% in *A. dumerili* (all measurements refer to the anterior-most tooth on the dentary). Furthermore, the ventral segment of the dentary is slightly longer in *Boa* than in *Acrantophis*.

Interestingly, *Sanzinia* presents the highest number of dentary teeth (up to 21 per row), despite having the shortest dentary overall (Figure 36). Moreover, the two species differ in tooth size, with *S. volontany* having longer dentary teeth (17% skull length) than *S. madagascariensis* (11.5%). In *Corallus*, the bone appears clearly thicker than in *Boa* and *Acrantophis*, with exceptionally large teeth as in the maxilla (19.5% skull length). However, the dentary only houses 13 teeth in this genus (Figure 36).

3.27 | Angular (Figures 37 and 39C)

The angular is thin and elongated in *Boa* and *Acrantophis*, which, however, differ in that the former presents three foramina on the bone as opposed to one in the latter

Compound bone
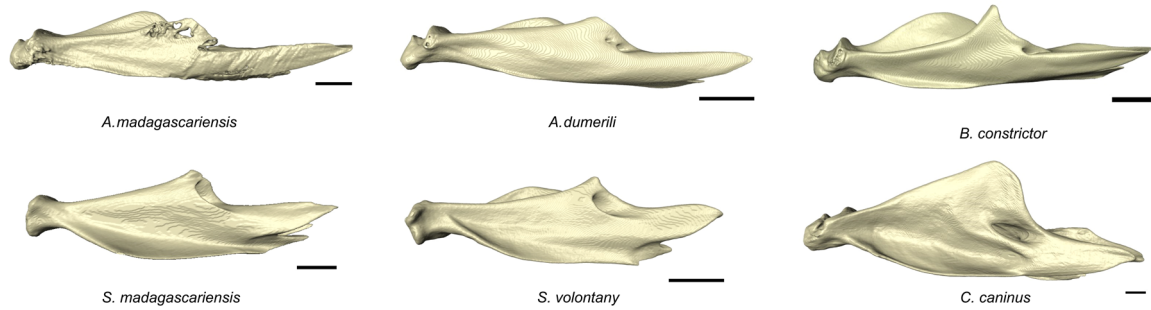
FIGURE 35 | Comparison of compound bones in lateral view. Scale bar = 5 mm.

Dentary
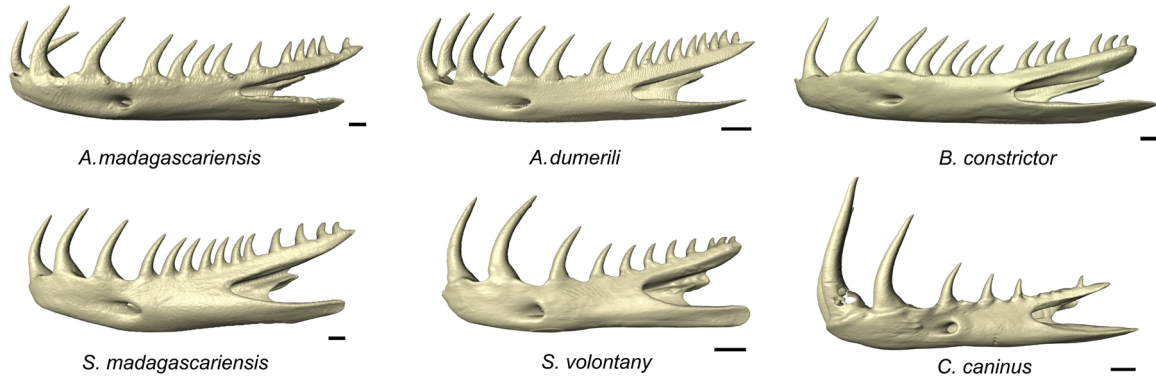
FIGURE 36 | Comparison of dentaries in lateral view. Scale bar = 2 mm.

Angular
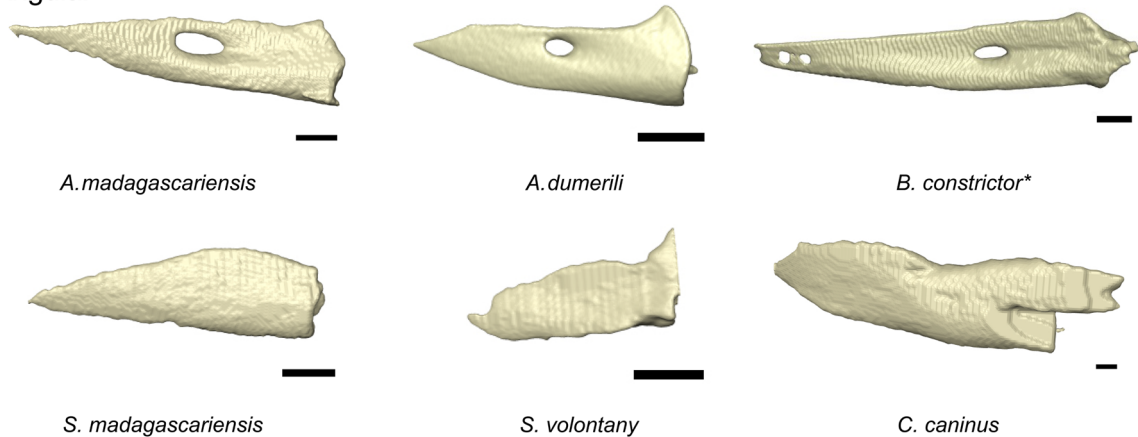
FIGURE 37 | Comparison of left angulars in medial view. *Right angular of *Boa constrictor* is shown due to damage of the left bone. Scale bar = 1 mm.

(Figures 37 and 39C). More specifically, one large foramen is found anteromedially and two smaller ones posteriorly in *Boa*. Furthermore, *Boa* and especially *A. dumerili* present a prominent process tapering into a crest laterally from the anterior section of the angular, which is considerably less pronounced in *A. madagascariensis* (Figures 37 and 39C). The angular is entirely different in both species of *Sanzinia*, where it is a short, triangular to ovoid bone devoid of foramina and processes (Figure 37). The angular gradually narrows posteriorly in *S. madagascariensis* as opposed to the uniform shape

observed in *S. volontany*. The angular appears roughly rectangular and compact in *Corallus* as well, with neither processes nor foramina (Figure 37). However, it should be noted that this bone was damaged in our specimen.

3.28 | Splenial (Figures 38 and 39D)

The splenial generally consists of a tall, thin posterior section culminating in a pronounced anterodorsal process,

Splenial

A. madagascariensis

A. dumerili

B. constrictor

S. madagascariensis

S. volontany

C. caninus
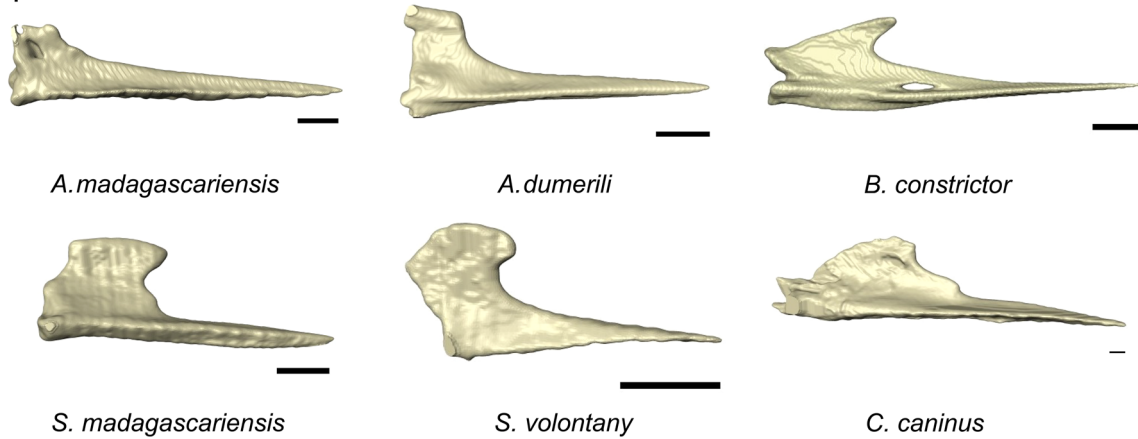
FIGURE 38 | Comparison of splenials in lateral view. Scale bar = 2 mm.
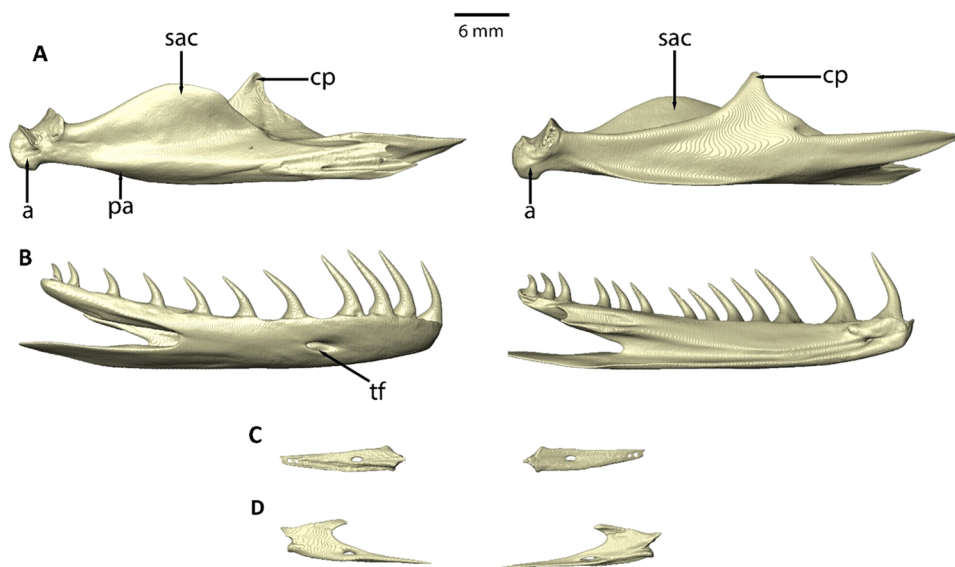
FIGURE 39 | Compound bone (A), angular (B), splenial (C), and dentary (D) of *Boa constrictor*. (A) left bone in medial view (left), right bone in lateral view (right); (B) right bone in lateral view (left), left bone in medial view (right); (C, D) right bone in lateral view (left), right bone in medial view (right). a = articular, cp = coronoid process, pa = prearticular process, sac = surangular crest, tf = foramen for mandibular branch of trigeminal.

which eventually narrows down anteriorly in an elongated lamina (Figures 38 and 39D). In *Boa*, the dorsal process is exceptionally prominent and results in a marked concavity in the posterior section of the bone, which also presents a narrow foramen. This pattern is common to *Acrantophis* as well (albeit with a straight dorsal process), which on the other hand presents a thicker anterior lamina. In *Corallus*, the anterodorsal process extends further along the medial section of the bone, presenting a smooth surface with no indentations (Figure 38). Consequently, the anterior lamina is comparably shorter than in *Boa* and *Acrantophis*, although markedly broader. The bone is overall strikingly long in *Corallus*. The two *Sanzinia* species display a remarkably tall and broad posterior section of the splenial, which is linear in *S. madagascariensis* but slightly concave in *S. volontany* due to a more pronounced anterodorsal process (Figure 38). In both species, the anterior lamina is markedly thin and narrow.

4 | Discussion

4.1 | Convergent Ecological Guilds Among Madagascan and American Booideans

Corallus caninus and *Sanzinia* present a large, funnel-shaped head, comparatively shorter than in *Boa* and *Acrantophis*, with longer teeth and considerably thicker jaws. Both *Corallus* and *Sanzinia* are at least semi-arboreal, with the former more arboreal than the latter (Borer 2013; Glaw and Glaw 2004; Pizzatto and Marques 2007a; Pizzatto, Almeida-Santos, and Shine 2007b). *Boa* is also semi-arboreal, whereas *Acrantophis* is more terrestrial despite strong morphological similarities (Glaw and Glaw 2004; Pizzatto, Almeida-Santos, and Shine 2007b). To better understand the extent and evolutionary drivers of the convergence of American and Madagascan booideans, we searched the literature for dietary data on *Boa*, *Corallus*, *Sanzinia*, and *Acrantophis*. Our findings show that both *Sanzinia* and *Acrantophis* feed most frequently on

mammals. The size of the snake also appears to be a relevant factor, as larger species tend to consume larger prey items (e.g., adult lemurs). More specifically, *A. madagascariensis* is a known predator of multiple species within Lemuroidea, whereas the smaller *A. dumerili* feeds primarily on rodents (see supplementary online material references). *Boa constrictor*, on the other hand, is the most markedly generalist among the taxa studied, with consumed prey ranging from iguanas to monkeys and parrots.

Surprisingly, we found scant evidence that arboreal booideans (except *C. hortulanus*) consistently feed on avian prey, which has been suggested as the adaptive reason behind the evolution of stronger jaw muscles and longer teeth in these snakes (Knox and Jackson 2010). Our results, therefore, support Henderson, Pauers, and Colston (2013), who already questioned the alleged preference for avian prey in arboreal booideans due to the snakes most often pointing downward rather than upward when in striking position. Although *C. caninus* differs from most *Corallus* species in being an ambush predator rather than an active forager (Henderson and Pauers 2012; Henderson, Pauers, and Colston 2013), no member of the genus is known to be a strict bird specialist (Henderson and Pauers 2012; Pizzatto, Marques, and Facure 2009), with *C. hortulanus* feeding equally frequently on birds and mammals according to the literature. However, Henderson, Pauers, and Colston (2013) report that the larger *Corallus* species such as *C. caninus* (which are characterized by long heads and strong jaw muscles) mainly prey on large mammals compared to their size. Our results confirm this and show a similar pattern for *Sanzinia*, which further supports a potential convergent evolutionary event. However, *Sanzinia* is not as strictly arboreal as *Corallus*, and neither *C. caninus* nor *C. hortulanus* might represent the best ecomorphological comparison for *Sanzinia* in the Neotropics. A similar comparison between *Sanzinia* and the intermediate *Corallus* morphotype of Henderson, Pauers, and Colston (2013), for example, *C. ruschenbergerii*, would likely clarify the ecomorphological position of *Sanzinia* within the spectrum defined for *Corallus*.

In terms or nutritional payoff and handling costs, adult birds are usually not among the most advantageous prey items available for snakes, unlike mammals. This is because birds have a comparably lower relative prey mass (RPM, ratio of prey weight to snake weight) despite retaining a considerable relative prey bulk (RPB, combination of cross-sectional dimensions and deformability against snake gape width) due to their feathers and non-uniform body plan (Greene and Wiseman 2023). Thus, the nutritional return of a successfully ingested bird would likely be inferior to that of a mammal or nonavian reptile of equal RPM even for arboreal snake predators (e.g., the *Corallus* genus), especially if the evolutionary effort required to subdue and ingest it (e.g., constriction and mouth gape width) is considered. However, birds do feature consistently in *B. constrictor* and *C. hortulanus* feeding records, perhaps due to seasonal factors (e.g., high availability in certain time windows due to migratory patterns) and/or easier procurement of birds compared to mammals for arboreal foragers (although plenty of arboreal mammals such as primates regularly fall prey to booideans).

While mammals of a wide size range appear to be a basic food in the diet of Malagasy and Neotropical booideans alike, lizards are strongly represented as well. Although normally smaller and less bulky than mammals (which implies lower RPM), squamates generally share an elongated body plan that makes them relatively easy to engulf and ingest (Greene and Wiseman 2023). Thus, these animals might be a reliable food source, albeit not as nutritious as mammals of equal size. Large booideans such as adult *B. constrictor* and *A. madagascariensis* are further capable of subduing and ingesting large lizards, for example, green iguanas (*Iguana iguana*) and Madagascan iguanas (*Oplurus* sp.), respectively, which are likely to provide substantial nutritional payoffs thanks to their high RPM. Moreover, lizards are often readily available both in terrestrial and arboreal settings (as are mammals), which adds to their suitability as prey items for snakes hunting in either ecological niche (Greene and Wiseman 2023).

We note that *B. constrictor* appears to hunt indiscriminately in trees and on the ground, in line with its well-known semi-arboreal ecology (Pizzatto and Marques 2007a; Pizzatto, Almeida-Santos, and Shine 2007b). However, *Acrantophis* seems to forage mainly (albeit not exclusively) on the ground, despite a markedly *Boa*-like skull ecomorphotype that could in theory be compatible with semi-arboreality. Likewise, there are records of terrestrial hunting for *S. madagascariensis* (Borer 2013). Thus, the arboreal-terrestrial dichotomy is not absolute; a promising avenue of future work would be to look at comparative performance of jaw shapes for terrestrial and arboreal prey of different sizes. These snakes are well-suited to laboratory studies, which are likely to yield more useful insights than the fragmentary knowledge gathered over decades of chance observations.

Morphologically speaking, the most pronounced difference between the more terrestrial and arboreal genera in our study relates to the depth of the bones of the jaw (particularly the dentary and compound bone) and length of the anterior teeth, matching an overall pattern across most alethinophidians (Knox and Jackson 2010). In booids, the anterior teeth do not immediately stab the prey, but slide over it and pierce only when the prey is fully grasped (Cundall and Deufel 1999; Deufel and Cundall 1999). The striking mechanisms and tooth morphology of *B. constrictor*, with the anterior teeth more recurved than the posterior to "slide" over the prey and stab it only after the jaws close (Ryerson and Van Valkenburg 2021) is shared with *Corallus* and the Madagascan boas as evidenced by our scans as well as previous literature (Cundall and Deufel 1999). However, Deufel and Cundall (1999) reported variability in strike dynamics across seven booid species in terms of first point of contact with the prey and subsequent head rotation, albeit without testing for arboreal predation. The importance of grasping against struggling prey is likely to be greater for arboreal constrictors, where a significant portion of the snake's body is involved in physical support and not available for constriction. Jayne (1982) found the *spinalis-semispinalis* muscular complex (the structure responsible for constriction, among other functions) to be shorter in proportion to body length in arboreal snakes than in terrestrial ones, with muscle strength being inversely proportional to muscle length. This likely serves the double purpose of being an adaptation to climbing, as well as having greater constricting force with a smaller fraction of the body, enabling effective constriction from arboreal perches.

Especially interesting are recent works on the dynamics of striking and constriction in *B. constrictor*, which—unlike the exclusively terrestrial ball python (*Python regius*)—was shown

in lab experiments to adapt to arboreal predation by positioning the prey in the direction of gravity and supporting its weight with supplemental loops of its body to facilitate swallowing (Ryerson, Sweesy, and Goulet 2022). It is worth noting that *B. constrictor* is one of the largest booids, with the nominate subspecies (*B. c. constrictor*) attaining lengths beyond the 4 m mark (Glaw and Franzen 2016). This might allow *B. constrictor* to make up for weaker jaw muscles compared to fully arboreal booids (e.g., *C. caninus*) by devoting supplemental coils of its body to prey restraint and facilitating the swallowing process thanks to gravity. Available reports summarized herein show that *B. constrictor* is capable of coiling in one to three loops around the prey based on the latter's size as well as its own (see Supporting Information S2: Table 1). However, arboreal boas such as several *Corallus* species are also known to employ a similar constriction and swallowing strategy (Supporting Information S2: Table 1), further emphasizing the need for further research on jaw and body musculature in booideans and its influence on prey handling.

Finally, it is worth noting that the adaptations toward either arboreality or terrestriality described above for booideans are broadly shared with another major lineage of large-bodied constrictors, the Australasian pythonids, and especially the genera *Liasis* and *Morelia* (Esquerré and Keogh 2016; Pyron, Reynolds, and Burbrink 2014). The repetition of these remarkably distinct guilds resembles, at a far greater geographical scale, the ecological guild evolution observed in adaptive radiations on islands or in lakes (Brawand et al. 2014; Losos et al. 1998; Mahler et al. 2013; Ronco et al. 2021; Sturmbauer 1998), suggesting some degree of determinism in ecomorphological guild divergence of these snakes. Given these three replicates of arboreal-terrestrial divergence, it is tempting to suggest that this represents one of the major axes of least resistance (McGlothlin et al. 2018) for booidean diversification (Esquerré and Keogh 2016), but we emphasize the importance of the role of ecological opportunity and chance, that is, contingency, in such radiations. This is further compounded by the small sample size available from such small radiations; patterns in groups with either low rates of diversification or high rates of extinction are more difficult to infer than those in large radiations, like those in colubroid snakes or anoles.

The differences in skull morphology observed between terrestrial and (semi)arboreal taxa are probably not linked to specific dietary preferences driven by one particular niche (e.g., arboreality supposedly favouring predation on birds) but rather to the niche itself, which would impose constraints on the snake's foraging strategy regardless of preferred prey types. This might extend to the evolution of supralabial thermosensitive pits or grooves, which are present in the *Corallus* and *Sanzinia* (but see Maderson 1970 for discussion of function in *Sanzinia*) but absent in *Boa* and *Acrantophis* (Lynn 1931; Ros 1935). Given the well-appreciated role these organs play in prey capture (Goris 2011; Laursen, Tang, and Garrity 2023), it is possible that *Sanzinia* and *Corallus* might be more reliant on them due to otherwise poor visibility at nighttime, although *B. constrictor* does possess thermoreceptors under its supralabial scales as well (von Düring 1974).

If corroborated by further work (especially comparative phylogenetic analyses), the pattern of convergent evolution in skull morphology described herein will align with the dynamics observed in

booids as a whole and pythonoids (Esquerré and Keogh 2016), natricines (Deepak, Gower, and Cooper 2022), and scolecophidians (Strong, Scherz, and Caldwell 2022), although dietary specialization did influence morphology to varying extent in these clades. Therefore, we call for an in-depth morphometric analysis on a larger sample of booidean species to determine the extent to which dietary specialization and/or habitat characteristics shape skull morphology in these snakes.

4.2 | Taxonomic Confusion Caused by Evolutionary Convergence in Malagasy and Neotropical Booideans

In Appendix 1, we provide a detailed list of the 67 characters that led Kluge (1991) to the conclusion that the Madagascan boas should be transferred to the genus *Boa* and compare them to our own findings. Although 13 characters were found to differ from the states that he gave (mostly in *Sanzinia*), we confirm most of Kluge's observations, and it remains true that these traits are indeed shared by *Boa* and the Sanziniidae. However, as already observed by Burbrink (2005), more than half (48/79) of the characters used by Kluge are subject to homoplasy, and therefore are misleading for phylogenetic inference.

Our study largely confirms the description of the skull of *Sanzinia* by Genest-Villard (1966), the only noticeable difference being the length of the supratemporal (described as exceptional in said work, yet shorter than in *Boa* and *Acrantophis* as evidenced here). Although a bone-by-bone comparison between our results and Genest-Villard's is beyond the scope of this paper, the overall high similarity reinforces the strength of our findings.

In light of the insurmountable genetic evidence for only distant relationship of Madagascan and Neotropical booideans (Burbrink 2005; Reynolds et al. 2014; Noonan and Chippindale 2006; Pyron et al. 2013, 2014; Vences et al. 2001; Vences and Glaw 2003), the patterns highlighted in this study reveal remarkable convergent evolution. Features that we believe are related to functional ecology far outnumber traits that suggest shared ancestry, leading to an overall impression of similarity between *Corallus* and *Sanzinia* (*Sanzinia* skulls distinctly do not resemble *Boa* skulls), and between *Boa* and *Acrantophis*. This convergence historically led to extensive trouble with taxonomic placement, with the likes of Boulenger (1893), for example, placing *S. madagascariensis* within *Corallus* and *Acrantophis* within *Boa*. Finally, we identified a potential synapomorphy exclusive to the Sanziniidae in the palatine dentition, which is articulated in two rows as opposed to a single row in *Boa* and *Corallus*.

5 | Conclusions

This study aimed to shed light on the potential evolutionary drivers behind morphological affinities and differences between the four Madagascan boas (Sanziniidae, genera *Acrantophis*, and *Sanzinia*) and the Neotropical booidean radiation (represented by *B. constrictor* and *C. caninus*) long thought to be each other's sister lineages or even congenerics. Overall, our

findings confirm previous reports of extensive similarities in cranial morphology between *Boa*, *Sanzinia*, and *Acrantophis*, which represent a remarkable case of convergent evolution.

Based on available records of dietary preferences for these snakes, we propose that the shared traits observed in prevalently arboreal (*Sanzinia* and *Corallus*) versus mainly terrestrial (*Acrantophis* and *Boa*) genera, regardless of geographic origin, are tied to their preferred ecological niche. More specifically, (semi-)arboreal species tend to have longer teeth and thicker/broader mandibles supporting strong muscles to grab and hold prey items as they cannot rely on the entire length of their body for constriction while hanging from tree branches. However, *B. constrictor* forage on the ground and in the canopy alike despite its "terrestrial-like" cranial morphology, hinting at a possibly more complex dynamic at play that should be the focus of future research. Instances of arboreal and terrestrial foraging are also documented for *Acrantophis* and *Sanzinia*, respectively.

Taken together, these nuances underscore the need for research studies using techniques such as geometric morphometrics combined with large-scale natural history surveys and observations of predation/constriction in a controlled setting to document the dietary habits of these booidean lineages. Thus, the present work adds to the body of knowledge concerning relationships between separate lineages of booidean snakes and advocates for ecological explanations behind convergence in cranial morphology across distantly related species. Furthermore, the first complete description of the skull of *B. constrictor* is provided, highlighting how the anatomy of even such an iconic snake species still presents knowledge gaps that warrant future research efforts.

Author Contributions

Conceptualization: Mark D. Scherz, Frank Glaw, Lorenzo Seneci. *Investigation and data processing*: Lorenzo Seneci, Mark D. Scherz, Frank Glaw. *Wrote original draft and made images*: Lorenzo Seneci, Mark D. Scherz. *3D reconstructions*: Lorenzo Seneci, Alexander S. Hall. *Edited final manuscript*: All authors.

Acknowledgments

Conflicts of Interest

Alexander S. Hall is employed by Thermo Scientific, who also supplies the software used for visualization and editing of scan images in this study (Amira). The other authors declare no conflicts of interest.

Data Availability Statement

A database of predation records and gut content analysis with references is available in the supplementary online material of this article. Full views of all skulls (frontal, dorsal, lateral, ventral, and posterior) with bone labels are also available in the supplementary information. Raw micro-CT scanning data for all specimens used for this study is available in Morphosource at https://www.morphosource.org/projects/00000C522.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Appendix 1

Kluge's inclusion of the two Madagascan taxa in the genus *Boa* was based on their sharing of the following morphological characters out of the 79 he examined (characters shared by all boines were excluded from this list for the sake of brevity):

Character no. 2 (Premaxilla)—*The dorsal-anterodorsal margin of the ascending nasal process of the premaxilla is slightly wider than the body of the process*. This is confirmed by our analysis.

Character no. 3 (Premaxilla)—*The dorsal margin of the transverse process of the premaxilla, adjacent to the nasal process, is thick and little, if at all, elevated*. This state was not observed in the analyzed specimens, where the margin appeared considerably thinner dorsally than ventrally.

Character no. 5 (Premaxilla)—*The transverse process of the premaxilla is directed horizontally or downward*. This is true for the part of the transverse process located proximally with respect to the ascending process, but in both *Sanzinia* and *Acrantophis*, the distal section of the transverse process is curved upward. The process appears roughly horizontal in *Boa*, thereby confirming Kluge's observations for this genus.

Character no. 8 (Premaxilla)—*The base of the nasal process of the premaxilla is narrow and abuts nearly vertically, or it inserts between, the nasal laminae*. This is confirmed for *Boa* and *Acrantophis*, while *Sanzinia* does not present such a characteristic; the nasal process is separated by a considerable distance from the nasal laminae in this genus.

Character no. 9 (Premaxilla)—*The floor of the premaxilla, the horizontal area formed by the united anterior portion of the vomerine processes, is narrow*. This character is confirmed for *Boa*, whereas *Sanzinia* and *Acrantophis* present a considerably wider area in proportion.

Character no. 11 (Nasal)—*The anterior margin of the ventral lamina of the nasal, viewed laterally, is indented*. This is confirmed by our analysis.

Character no. 12 (Nasal)—*The anterolateral margin of the horizontal lamina of the nasal, viewed dorsally, is noticeably indented*. This is confirmed by our analysis.

Character no. 13 (Nasal)—*Much of the lateral margin of the horizontal lamina of the nasal, anterior to the prefrontal, lies at an angle to the midline*. This is confirmed by our analysis.

Character no. 14 (Nasal)—*The horizontal lamina of the nasal does not overlap the dorsal surface of the frontal*. This is confirmed by our analysis.

Character no. 15 (Nasal)—*The nasal contacts the frontal predominantly ventral to the mesial frontal flange suture*. This is confirmed only for *Boa*, as the two Madagascan genera do not present any contact between the nasal and the frontal.

Character no. 17 (Maxilla)—*The anterior three to four maxillary teeth are short, and if long, they are curved posteriorly*. The anteriormost teeth in all our specimens were the longest, but not the most evidently curved posteriorly (the curve is, however, noticeable). Therefore, this character is not confirmed by our analysis.

Character no. 18 (Maxilla)—*The lateral edge of the maxilla beneath the orbit is round or slightly inflected laterally*. This is confirmed by our analysis, as a lateral inflection was detected on the lateral edge of the maxilla beneath the optical cavity.

Character no. 19 (Maxilla)—*The suborbital region of the maxilla is shallow*. From our analysis, it is not clear whether *Sanzinia* presents this characteristic or not. The feature is, however, confirmed for *Boa* and *Acrantophis*.

Character no. 20 (Maxilla)—*The postorbital region of the maxilla is shallow, tapering gradually to a point*. This is confirmed for *Boa* and *Acrantophis*, but the maxilla does not extend beyond the orbit in *Sanzinia*.

Character no. 21 (Maxilla)—*From a dorsal view, the caudal end of the maxilla is directed posteriorly*. This is confirmed for *Acrantophis*, whereas in *Boa* and *Sanzinia,* the caudal end of the maxilla is directed posterolaterally.

Character no. 22 (Maxilla)—*Most of the palatine process of the maxilla occurs posteriorly, within the orbit*. This is confirmed by our analysis.

Character no. 24 (Prefrontal)—*Viewed dorsally, the lateral foot process of the prefrontal lies within the boundary of the underlying maxilla*. This is confirmed by our analysis.

Character no. 25 (Frontal)—*The interorbital width of the frontals is narrow*. This is not confirmed by our analysis, as the frontals cover a broad extension between the two orbits.

Character no. 26 (Frontal)—*The right and left supraorbital margins of the frontals are parallel or diverge*. This is confirmed by our analysis.

Character no. 28 (Postorbital)—*At least a major part of the dorsal one-third of the postorbital, above the accessory lobe, is uniformly broad*. This is confirmed by our analysis.

Character no. 29 (Postorbital)—*In lateral view, the ventral one-third of the postorbital is narrow*. This is confirmed for *Boa* and *Acrantophis*, whereas in *Sanzinia,* the postorbital conserves a constant width throughout its ventral extension.

Character no. 31 (Optic foramen)—*The posterior and dorsal margins of the optic foramen are flat or bounded by a low and rounded wall*. This is confirmed by our analysis.

Character no. 34 (Ectopterygoid)—*The ectopterygoid is oriented anteriorly*. This is confirmed by our analysis.

Character no. 35 (Ectopterygoid)—*The ectopterygoid lies dorsal to the maxilla*. This is confirmed by our analysis except for *Sanzinia volontany*, whereby the ectopterygoid lies behind the maxilla.

Character no. 37 (Ectopterygoid)—*The area of contact between the ectopterygoid and the pterygoid is relatively simple, flat, or composed of no more than one concave–convex facet*. This is confirmed by our analysis.

Character no. 39 (Parietal)—*The dorsolateral region of the parietal, between the postorbital and supratemporal, is bulbous*. This is confirmed by our analysis.

Character no. 40 (Parietal)–*The anterolateral corner of the parietal extends much beyond the lateral margin of the frontal*. This is confirmed by our analysis. However, this feature is considerably more evident in *Boa* than in the Madagascan genera.

Character no. 41 (Parietal)—*From a dorsal view, the posterior margin of the parietal, on the midline, forms an extremely long process*. This is confirmed by our analysis.

Character no. 43 (Supraoccipital)—*The midsagittal crest of the supraoccipital is only partly covered by the parietal midsagittal crest*. This is confirmed for *Boa* and *Acrantophis*. Conversely, in *Sanzinia*, the parietal midsagittal crest covers the supraoccipital one almost entirely.

Character no. 44 (Supratemporal)—*From a dorsal view, the supratemporals diverge*. This is confirmed by our analysis.

Character no. 45 (Supratemporal)—*From a lateral view, the supratemporal is inclined slightly*. This was not observed in the Madagascan taxa, which present a straight supratemporal in lateral view. No statement can be formulated for *Boa* as the quadrates of our specimen were broken, thereby modifying the supratemporal's orientation.

Character no. 47 (Stapes)—*The stapes does contact the quadrate*. This cannot be assessed in our analysis, as the stapes (columella in this paper) is not ossified distally.

Character no. 48 (Vomer)—*The horizontal posterior lamina is horizontal*. This is confirmed in all genera except *Corallus*, which presents a nearly vertical posterior lamina.

Character no. 49 (Septomaxilla)—*The lateroventral edge of the septomaxilla forms a large blade posterior to the fenestra vomeronasalis externa*. This is confirmed by our analysis, although the size of the blade varies considerably between genera and species.

Character no. 51 (Palatine)—*The choanal process of the palatine is short and far removed from the vomer*. This is confirmed by our analysis

Character no. 54 (Pterygoid)–*An anteromedial palatine process on the pterygoid is present*. This is confirmed by our analysis.

Character no. 57 (Basisphenoid)—*A midventral keel is absent to only moderately elevated on the basisphenoid*. This is confirmed for *Acrantophis* only, as the midventral keel is remarkably pronounced in *Boa* and *Sanzinia*.

Character no. 60 (Coronoid)—*The coronoid contacts the splenial*. This is confirmed by our analysis.

Character no. 62 (Coronoid)—*The anterodorsal margin of the coronoid extends slightly or well beyond the surangular, such that it is clearly exposed when viewed laterally*. This is confirmed by our analysis, although the coronoid is considerably more exposed in *Boa* and *Acrantophis* than in *Sanzinia* in lateral view.

Character no. 64 (Prearticular)—*The dorsal margin of the prearticular, the area where the adductor posterior muscle inserts, is noticeably curved upward*. This is confirmed by our analysis.

Character no. 67 (Teeth)—*There are small numbers of adult teeth*. By "small numbers," Kluge meant 18–22 teeth. This is therefore confirmed by our analysis, as none of the examined specimens exceeded this number.