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RESEARCH ARTICLE

Comparative osteology and functional morphology of the forelimb of *Cyonasua* (Mammalia, Procyonidae), the first South American carnivoran

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Abstract

Extant procyonids only inhabit the Americas and are represented by six genera (*Procyon*, *Nasua*, *Nasuella*, *Bassaricyon*, *Potos*, and *Bassariscus*); all of them, except *Bassariscus*, are present in South America. The first records correspond to the early Miocene in North America (NA) and the late Miocene in South America (SA). *Cyonasua* was the first carnivoran to enter SA from NA, before the Great American Biotic Interchange, and went extinct in the early middle Pleistocene. This extinct procyonid is recorded in several localities of Argentina, and also in Venezuela. Paleobiological studies of procyonids are interesting from evolutionary and biogeographical viewpoints. In this study, the pectoral girdle and forelimb of 10 specimens of *Cyonasua* are described and compared with extant South American procyonids using a qualitative approach. Additionally, four functional morphology indexes were calculated for them and compared with an ecologically diverse sample of living carnivorans. Results indicate that *Cyonasua* most resembles *Nasua nasua* and *Procyon cancrivorus*, even though the extinct procyonid possessed peculiar features. *Cyonasua* had robust and relatively short forelimb bones, with strong stabilized joints, and movements associated with the sagittal plane, which suggest a tendency toward terrestrial habits, related to their ability to resist relatively high bending and shearing stresses. However, some features indicate a freedom in their range of movements, with moderate supination ability, compatible with climbing. When combined with previous analyses of dietary habits and estimated body mass, the morphology of *Cyonasua* would be well suited for digging and prey manipulation, allowing them to prey on small and relatively large-sized vertebrates, as well as to avoid some of the predators that were dominant in the Cenozoic of South America.

KEYWORDS
Carnivora, locomotor mode, morphofunctional analysis, paleobiology, procyonids, substrate preference

1 | INTRODUCTION

The family Procyonidae includes six extant genera (*Procyon*, *Nasua*, *Nasuella*, *Bassaricyon*, *Potos*, and *Bassariscus*) with 13 species that only occur in the Americas, although *Procyon lotor* has been introduced into some Eurasian countries, especially by escaped captive individuals (Lotze & Anderson, 1979; Wilson & Mittermeier, 2009). All genera except *Bassariscus* are present in South America (Wilson & Mittermeier, 2009). Procyonids are ecologically diverse, small to medium-sized animals (1–8.5 kg) that occupy a variety of habitats, primarily those with some degree of arboreal cover. All species are able climbers (Wilson & Mittermeier, 2009). Within this diversity, species of *Nasua*, *Nasuella*, and especially *Procyon* spend most of the time on the ground (where they browse for food, mates, etc.), while *Potos* and *Bassaricyon* are exclusively arboreal. Only *Nasua* and *Nasuella* dig using their front paws and browse by digging small holes in the ground to capture prey (Beisiegel, 2001; Gompper & Decker, 1998; McClearn, 1992; Nowak, 2005; Wilson & Mittermeier, 2009). Most taxa are crepuscular and nocturnal, except for the diurnal *Nasua*, and omnivorous, but their wide dietary range also includes preferentially carnivorous (e.g., *Bassariscus*) or frugivorous (e.g., *Potos*) taxa (Gompper & Decker, 1998; Wilson & Mittermeier, 2009).

The geographical distribution of the family was wider in the past. Procyonids first appear in Europe, represented by the species *Pseudobassaris riggsi* Pohle, 1917 known from late Oligocene of France (Fulton & Strobeck, 2007; Koepfli et al., 2007; McKenna & Bell, 1997; Wolsan, 1993; Wolsan & Lange-Badré, 1996). However, the phylogenetic position of this taxon has engendered much debate (e.g., Finarelli, 2008; Sato et al., 2012; Wang, McKenna, & Dashzeveg, 2005).

They are first recorded in North America in the early Miocene, and the fossil record indicates that they entered South America from North America (Baskin, 1998) in at least two separate events (Cook & MacDonald, 1962; Forasiepi et al., 2014; Prevosti & Soibelzon, 2012; Rodriguez et al., 2013), first during the late Miocene (~7 MYBP), before full emergence of the Panamanian Isthmus, as part of the so-called proto-GABI (proto-Great American Biotic Interchange, sensu Cione, Gasparini, Soibelzon, Soibelzon, & Tonni, 2015). This first event involves four extinct genera: *Cyonasua*, *Chapalmalania*, *Parahyaenodon*, and *Tetraprothomo*, that is, the "*Cyonasua* group" (sensu Baskin, 2004, see also Patterson & Pascual, 1968). They were last recorded at the early middle Pleistocene (*Cyonasua meranii*; Soibelzon, Zurita, Gasparini, & Soibelzon, 2008; Tarquini, Vilchez-Barral, & Soibelzon, 2016). The second immigration event probably took place during the late Pleistocene–Holocene, and includes the extant South American taxa (see Lessa, Cartelle, Faria, & Gonçalves, 1998; Rodriguez et al., 2013; Soibelzon et al., 2010; Webb, 1985; and articles cited therein). However, Ruiz-Ramoni, Rincón, and Montellano-Ballesteros (2018) suggest that a record of *Nasua* and *Procyon* from El Breal of Orocual, Venezuela, is the oldest for these taxa (Marplatan, late Pliocene). It is important to point out that there is no evidence to support a late Pliocene age for the fossil procyonids discovered at El Breal of Orocual.

The record of *Cyonasua* Ameghino, 1885 is exclusively South American, with most specimens found in Argentina and a single one in Venezuela (Forasiepi et al., 2014). Their temporal record spans from the late Miocene (Fm. Andalhuala, Catamarca province of Argentina) to the early Pleistocene (Fm. Ensenada, Buenos Aires province of Argentina; Soibelzon, 2011; Soibelzon et al., 2008; Soibelzon & Prevosti, 2007, 2012; Tarquini et al., 2016). It encompasses 10 species, *C. argentina* Ameghino, 1885; *C. brevirostris* (Moreno & Mercerat, 1891); *C. longirostris* (Rovereto, 1914); *C. pascuali* Linares, 1981; *C. groeberi* Kraglievich & Reig, 1954; *C. lutaria* (Cabrera, 1936); *C. clausa* (Ameghino, 1904); *C. robusta* (Rovereto, 1914); *C. argentinus* (Burmeister, 1891), and *C. meranii* (Ameghino & Kraglievich, 1925; Soibelzon, 2011; Tarquini et al., 2016). Despite the number of named *Cyonasua* species, specimens are relatively scarce and most remain unpublished (Soibelzon, 2011).

Cyonasua had a wide range of body mass (12.5–28.4 kg), which was estimated using allometric equations of the postcranial skeleton (Tarquini, Toledo, Soibelzon, & Morgan, 2018) and skull following Van Valkenburgh (1990) (Prevosti & Forasiepi, 2018; Wroe, Argot, & Dickman, 2004). Both, postcranial and cranial estimates, yielded similar values, while estimates based on molars were strikingly different. This wide range is to be expected given the great diversity observed within the genus (Tarquini et al., 2018). The dental morphology of *Cyonasua* suggest an omnivorous diet, potentially even hypocarnivore to mesocarnivore (Prevosti & Forasiepi, 2018; Soibelzon, 2011).

Although the postcranial skeleton of *Cyonasua* was described in systematic studies (Ameghino, 1908; Bordas, 1942; Cabrera, 1936; Forasiepi, Martinelli, & Goin, 2007; Hrdlicka, 1912; Kraglievich & Reig, 1954; Rovereto, 1914), it has been relatively poorly studied from a paleobiological perspective (Soibelzon, 2011; Tarquini et al., 2018; Tarquini, Toledo, Morgan, & Soibelzon, 2017).

Using a quantitative approach, Tarquini et al. (2017) proposed that *Cyonasua* presents a combination of morphological traits different from those of extant procyonids, and that it was not a specialized form but rather generalized, with some degree of grasping ability compatible with climbing, and some digging capacity as well. In order to further explore these hypotheses, we use qualitative and quantitative analyses of a larger sample of *Cyonasua* specimens and compare it with other carnivorans.

We present an exhaustive description of the pectoral girdle and forelimb elements of *Cyonasua* in the context of the correlation between form and function, proposed by Radinsky (1987) and applied in numerous paleobiological studies of the postcranial skeleton (e.g., Andersson, 2004a; Argot, 2001, 2003, 2010; Argot & Babot, 2011; Candela & Picasso, 2008; Ercoli, Prevosti, & Álvarez, 2012; Hildebrand, 1988; Taylor, 1970, 1974, 1976, 1989; Toledo, Bargo, & Vizcaíno, 2013, 2015; Vizcaíno, Bargo, & Fariña, 2008). We also discuss and elaborate palaeocological hypotheses about the role of *Cyonasua* in the late Cenozoic communities of South America.

2 | MATERIALS AND METHODS

2.1 | Repository abbreviations

AMNH, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, USA; MACN-Ma, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Colección de Mastozoología, Ciudad Autónoma de Buenos Aires (CABA), Argentina; MACN-Pv, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," División Paleontología de Vertebrados, CABA, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia," Mar del Plata, Argentina; MNHN, Museo Nacional de Historia Natural de Montevideo, Uruguay; MNRJ: Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil; USNM, United States National Museum, Smithsonian Institution, Washington DC, USA; ZOOBA-M, Jardín Zoológico de Buenos Aires, Colección de Biomateriales, CABA, Argentina; ZVC-M, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay.

2.2 | Fossil specimens

The descriptions and comparisons of forelimb and pectoral girdle bones are based on 10 fossil specimens of *Cyonasua* sp. with associated postcranial elements (Supporting Information Table S1).

2.3 | Extant specimens

The morphology of each bone of the scapular girdle and forelimb of the fossil material was described and compared with extant South American procyonid species: *Procyon cancrivorus*, *Nasua nasua*, *Nasuella olivacea*, *Bassaricyon alleni*, *Bassaricyon gabbii*, *Bassaricyon* *medius*, *Bassaricyon neblina* and *Potos flavus* (see Supporting Information Table S2) by means of direct observation and binocular microscope.

2.4 | Anatomical descriptions

Anatomical terminology mostly follows the Nomina Anatomica Veterinaria (International Committee on Veterinary Gross Anatomical Nomenclature, NAV, 2012), but also other works on carnivoran anatomy (e.g., Davis, 1964; Evans & de Lahunta, 2013; Lessertisseur & Saban, 1967; Sisson & Grossman, 1985).

Unfortunately, for some SA procyonid specimens, comparisons for the autopodium were based on articulated bone elements, and some were missing from the collections.

2.5 | Indices of functional morphology

Four morpho-functional indices were calculated for the humerus and ulna, most of which were taken from the literature whereas one was designed for this work (see below). For this purpose, seven linear measurement taken with a digital caliper (0.01 mm precision) from 167 specimens of carnivorans with diverse substrate preferences and locomotor mode, and substrate use (see Figure 1 and Table 1). Due to their preservation, only four fossil specimens could be included in this analysis: MACN-Pv 2914, MLP 35-X-4–4, MLP 04-VI-10-1, and FMNH P 14342.

Indices were analyzed by: (1) taxon, (2) substrate preference (SP) and locomotor mode (LM), and (3) substrate use (SU), and presented as box plots. These discrete categories were selected based on published information (see Table 1).

To test for allometry, permutation regressions of mean indices by taxa against log transformed average body mass (from literature, see Supporting Information Table S3) were performed using R statistical suite (R Core Team, 2018) using the *lmp* command of the package *lmPerm* (Wheeler & Torchiano, 2016).

2.5.1 | Humerus robustness index

HRI = transverse diameter at midshaft of the humerus (TDH)/humeral length (HL). This index indicates robustness of the humerus and estimates its ability to resist bending and shearing stresses (Chen & Wilson, 2015; Elissamburu & Vizcaíno, 2004; Samuels, Meachen, & Stacey, 2013; Samuels & Van Valkenburgh, 2008).

2.5.2 | Humeral distal end width index

HDEWI = humeral distal epiphysis width (HDEW)/humeral length (HL). This index describes the relative extension of the medial epicondyle (Chen & Wilson, 2015; Sargis, 2002), which provides surface area for the origin of major autopodial flexor muscles (Evans & de Lahunta, 2013). According to some authors (Elissamburu & Vizcaíno, 2004; Hildebrand, 1985; Samuels et al., 2013; Samuels & Van Valkenburgh, 2008; Toledo, Bargo, Cassini, & Vizcaíno, 2012; Vizcaíno, Fariña, & Mazzetta, 1999), high values of this index are considered a good indicator of digging abilities.

2.5.3 | Humeral condyle depth index

HCDI = humeral distal articular surface width (HDASW)/depth of humeral trochlea (DHT). This index was designed for this study. It reflects the extension of the trochlea. Lower values are associated with a relatively narrow and box-like condyle, which in turn is linked to a more stabilized elbow joint with relative restriction of movements to the parasagittal plane (Andersson, 2004a).

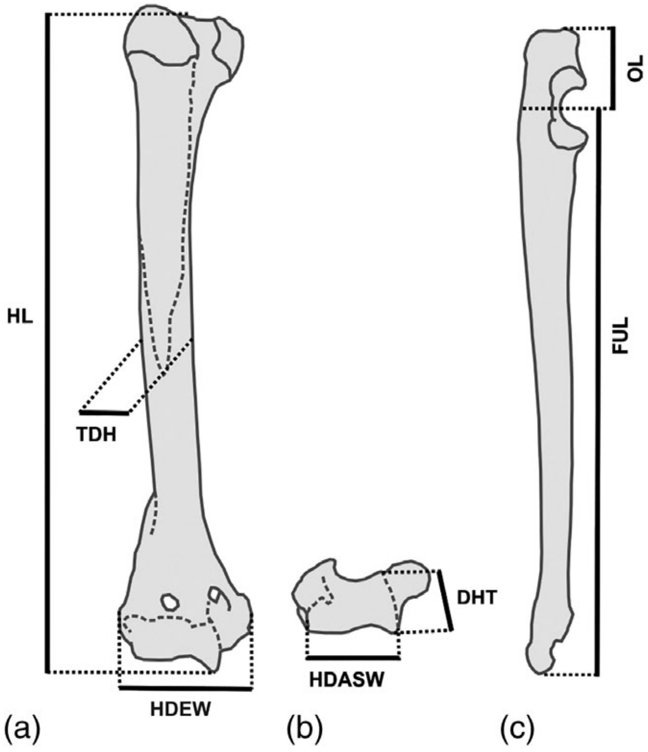

FIGURE 1 Forelimb measurements used to calculate the morpho-functional indexes. (a) cranial view of the humerus, (b) distal view of the humerus, (c) lateral view of the ulna. Abbreviations: DHT = depth of humeral trochlea; FUL = functional ulnar length; HDASW= humeral distal articular surface width; HDEW = humeral distal epiphysis width; HL = humeral length; OL = olecranon length; TDH = transverse diameter at midshaft of the humerus

2.5.4 | Index of Fossorial ability

IFA = olecranon length (OL)/ functional ulnar length (FUL). High values of this index are correlated with greater relative length of the in-lever arm (and hence of the mechanical advantage) of the *m. triceps brachii caput longum*, *laterale*, *mediale*, *accesorium*, and *mediale accesorium)* and *m. anconeus* during powerful elbow extension. Some authors have used this index as an indicator of digging ability (Chen & Wilson, 2015; Hildebrand, 1985; McClearn, 1992; Reese, Lanier, & Sargis, 2013; Samuels et al., 2013; Vizcaíno et al., 1999; Vizcaíno & Milne, 2002).

3 | RESULTS

3.1 | Description and comparisons of *Cyonasua* with extant south American procyonids

3.1.1 | Scapula

This element is partially preserved in only two fossil specimens: MLP 04-VI-10-1 and MACN-Pv 6689. The following description is based on the first specimen.

TABLE 1 Discrete categories for each taxon used to calculate the functional morphology indexes

Taxon	Substrate preference and locomotor mode (SP and LM)	Substrate use (SU)
Procyonidae		
Bassaricyon gabbii	Tree-dwellers[a]	Unspecialized/No[a]
Bassaricyon alleni	Tree-dwellers[a]	Unspecialized/No[a]
Bassaricyon medius	Tree-dwellers[a]	Unspecialized/No[a]
Bassaricyon neblina	Tree-dwellers[a]	Unspecialized/No[a]
Bassariscus astutus	Scansorial[a,b]	Unspecialized/No[a]
Nasua nasua	Scansorial[a]	Specialized[c]
Nasua narica	Scansorial[a]	Specialized[c]
Nasuella olivacea	Scansorial[a]	Specialized[a]
Potos flavus	Tree-dwellers[a,d]	Unspecialized/No[a]
Procyon cancrivorus	Terrestrial-climbers[a]	Unspecialized/No[a]
Procyon lotor	Terrestrial-climbers[a]	Unspecialized/No[a]
Ailuridae		
Ailurus fulgens	Scansorial[a]	Unspecialized/No[a]
Mustelidae		
Galictis cuja	Terrestrial-generalist[a]	Unspecialized/No[a]
Eira barbara	Scansorial[a]	Unspecialized/No[a,e]
Gulo gulo	Terrestrial-climbers[f]	Unspecialized/No[f]
Lontra longicaudis	Semiaquatic[a]	Unspecialized/No[a]
Lontra provocax	Semiaquatic[a]	Unspecialized/No[a]
Lyncodon patagonicus	Terrestrial-generalist	Unspecialized/no
Meles meles	Terrestrial-generalist[a]	Specialized[a]
Mephitidae		
Conepatus	Terrestrial-generalist[a]	Specialized[g,h]
Viverridae		
Arctictis binturong	Tree-dwellers[a]	Unspecialized/No[a]
Paradoxurus hermaphroditus	Scansorial[a]	Unspecialized/No[a]
Nandinidae		
Nandinia binotata	Tree-dwellers[a,i]	Unspecialized/No[a]
Ursidae		
Melursus ursinus	Terrestrial-climbers[a]	Unspecialized/No[a]
Tremarctos ornatus	Terrestrial-climbers[a]	Unspecialized/No[a]
Felidae		
Leopardus geoffroyi	Terrestrial-climbers[a]	Unspecialized/No[a]
Canidae		
Lycalopex gymnocercus	Terrestrial-cursorial[a]	Unspecialized/No[a]
Lycalopex griseus	Terrestrial-cursorial[a]	Unspecialized/No[a]
Lycalopex culpaeus	Terrestrial-cursorial[a]	Unspecialized/No[a]
Cerdocyon thous	Terrestrial-cursorial[a]	Unspecialized/No[a]
Chrysocyon brachyurus	Terrestrial-cursorial[a]	Unspecialized/No[a]

[a] Wilson and Mittermeier (2009)
[b] Trapp (1972)
[c] McClearn (1992)
[d] Van Valkenburgh (1987)
[e] Presley (2000)
[f] Pasitschniak-Arts and Larivière (1995)
[g] Castillo, Luengos-Vidal, Caruso, Lucherini, and Casanave (2013)
[h] Kasper, Soares, and Freitas (2012)
[i] Taylor (1974)

Because of its poor preservation, the overall shape of the scapula could not be determined; in extant SA procyonids, the shape of the scapular blade varies from subrectangular to rounded (Figure 2). In *Cyonasua* sp. the cranial border (*margo cranialis*) is more markedly deflected toward the lateral side than in extant SA procyonids, which also present this deflected margin (Figures 2 and 3). The surfaces of the supraspinous and subscapular fossae (*fossa supraspinata* and *fossa subscapularis*, respectively) are irregular and undulated, and the latter also bears grooves. However, in extant SA procyonids these surfaces are rather smooth. The coracoid process (*processus coracoideus*), almost completely preserved, is high and curved medially, similar to the condition of *N. nasua*, in which this process is larger and more medially directed than in the remaining procyonids (Figure 3a,d). In *N. olivacea*, *P. cancrivorus*, *Bassaricyon*, and *P. flavus* this *processus* forms a small dome-shaped prominence that is only slightly bent medially (Figure 3c,e–j).

The scapular spine (*spina scapulae*) of *Cyonasua* sp. is a strong element with irregular and wavy margins; and in contrast to extant species, it is more developed and more laterally projected (i.e., high scapular spine; Figures 2a and 3a). The ventral end of the scapular spine (*acromion*) in *Cyonasua* sp. presents a robust *processus hamatus* as in some extant procyonids such as *N. nasua*, *N. olivacea* and *B. medius* (Figure 2a,c,d,g). It extends ventrally to the level of the glenoid cavity (*cavitas glenoidalis*); whereas in most extant SA procyonids (except for *Bassaricyon alleni*) the *P. hamatus* extends beyond this cavity (Figure 2). Additionally, the *P. hamatus* of *Cyonasua* sp., as in *N. nasua*, *N. olivacea*, *Potos flavus*, and in almost all *Bassaricyon* species, is markedly oriented cranially; however, in *P. cancrivorus* and *B. neblina* the *P. hamatus* is extended distally in a straight line (Figure 2).

The glenoid cavity is slightly concave, between oval and pyriform, strongly similar to the morphology of *N. nasua* (Figure 3a,b,d). In contrast, this cavity is more concave in *N. olivacea*, slightly concave but more oval (cranio-caudally elongated) in *P. cancrivorus*, and markedly round and concave in *P. flavus* and *Bassaricyon*. The glenoid cavity in *Cyonasua* sp. is separated from the scapular blade by a relatively long neck (*collum scapulae*), similarly to the condition observed in *P. cancrivorus* (Figure 2a,b). The scapular neck is slightly shorter in *N. nasua* and *Bassaricyon*, shorter in *N. olivacea* and almost absent in *P. flavus* (Figure 2c–i). The supraglenoid tubercle (*tuberculum supraglenoidale*) of *Cyonasua* sp. is slightly more projected ventrally when compared with SA extant procyonids (Figure 2).

3.1.2 | Humerus

Only one nearly complete specimen, corresponding to the left humerus of FMNH P 14342, has been recorded so far, whereas more fragmentary humeri are known for several specimens: FMNH PM 20453, MACN-Pv 2914, MACN-Pv 6688, MACN-Pv 6689, MLP 04-VI-10-1, MLP 35-X-4-4, and MLP 29-X-8-18.

The humerus is a robust element in *Cyonasua* and its diaphysis is medially concave (Figure 4a). In contrast, the humeral diaphyses of extant SA procyonids are relatively gracile (e.g., *Bassaricyon*), ranging from moderately thin (e.g., *P. cancrivorus* and *P. flavus*) to moderately robust (e.g., *N. nasua* and *N. olivacea*; Figure 4i–m).

The humeral head (*caput humeri*) of *Cyonasua* presents a smooth and somewhat flat articular surface similar to that of *P. cancrivorus* (Figures 5a,b,f and 6a–c). In proximal view (Figure 6), the humeral head is longer than wide, more so than in the extant procyonids *N. nasua*, *N. olivacea*, and *P. cancrivorus*. The posterior apex projects posteriorly forming a well-marked inflexion of the neck (*collum humeri*) at the posterior side of the diaphysis; this last feature resembles that of *N. nasua* and *P. cancrivorus* (Figure 5a,b,f,g). In addition, FMNH P 14342 presents a humeral head caudally displaced relative to the diaphyseal axis, similar to the condition observed in *P. cancrivorus*, *N. nasua*, and *N. olivacea*; in contrast, this displacement is smaller in *Bassaricyon* and even more in *P. flavus*, in which the head is close to the diaphyseal axis (Figure 5). The greater and lesser tubercles (*tuberculum majus et minus*) of *Cyonasua* are almost at the same level and do not protrude beyond the head, as in *P. cancrivorus* (Figures 5 and 6). In all other SA procyonids both tubercles are located slightly below the proximal surface of the humeral head, and they are particularly low in *P. flavus* (Figure 6d–g). In contrast to all extant species examined, in *Cyonasua* the lesser tubercle is poorly developed medially and the greater tubercle is markedly protruding cranially (Figure 6a,b). The intertubercular groove (*sulcus intertubercularis*) is wide and shallow in

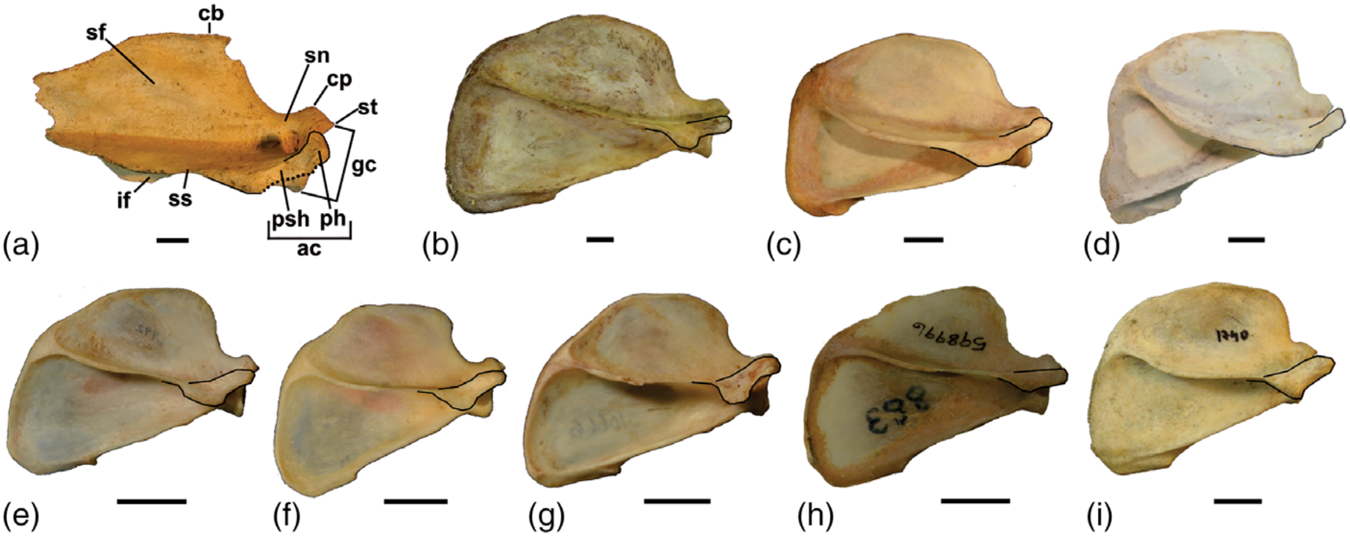

FIGURE 2 Lateral view of the scapula. (a) *Cyonasua* sp. MLP 04-VI-10-1, (b) *P. cancrivorus* MLP 1.I.03.25, (c) *N. nasua* AMNH 255871, (d) *N. olivacea* FMNH 70745 (inverted = inv.), (e) *B. alleni* USNM 396992, (f) *B. gabbii* AMNH 184985, (g) *B. medius* USNM 31066, (h) *B. neblina* USNM 598996, (i) *P. flavus* MLP 1470. Abbreviations: ac = acromion; cb = cranial border; cp = coracoid process; gc = glenoid cavity; if = infraspinous fossa; ph = *processus hamatum*; psh = *processus suprahamatum*; sf = supraspinous fossa; sn = scapular neck; ss = scapular spine; st = supraglenoid tubercle. The structure of the acromion is highlighted with a black line. Scale bars: 1 cm [Color figure can be viewed at wileyonlinelibrary.com]

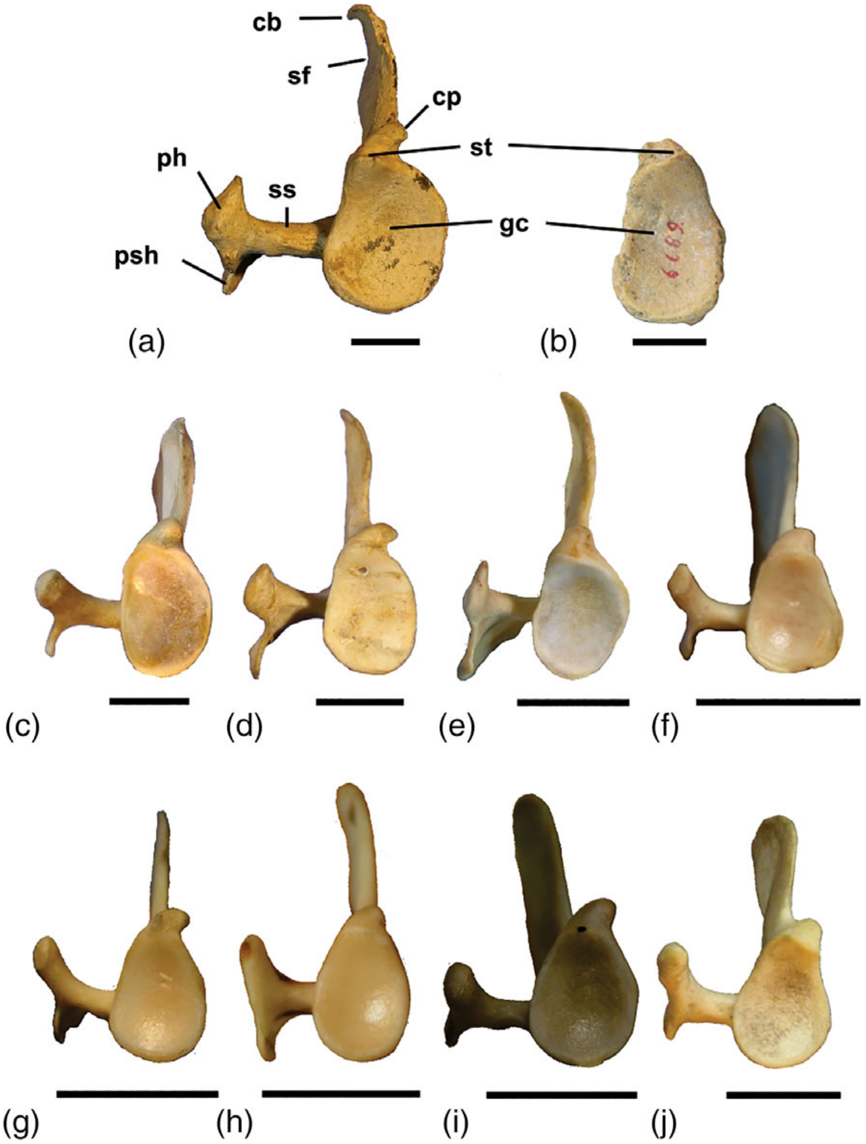

FIGURE 3 Distal view of the scapula. (a) *Cyonasua* sp. MLP 04-VI-10-1, (b) *Cyonasua* sp. MACN-Pv 6689, (c) *P. cancrivorus* MLP 2110, (d) *N. nasua* MACN-Ma 5.12, (e) *N. olivacea* FMNH 70745 (inv.), (f) *B. alleni* USNM 396992, (g) *B. gabbii* AMNH 184985, (h) *B. medius* USNM 305748, (i) *B. neblina* USNM 598996, (j) *P. flavus* MLP 1470. Abbreviations: cb = cranial border; cp = coracoid process; gc = glenoid cavity; ph = *processus hamatum*; psh = *processus suprahamatum*; sf = supraspinous fossa; ss = scapular spine; st = supraglenoid tubercle. Scale bars: 1 cm [Color figure can be viewed at wileyonlinelibrary.com]

FMNH P 14342, as in *N. nasua*, *N. olivacea*, *P. flavus*, *B. neblina*, and *B. medius* (Figure 6b,d–g); whereas in MLP 04-VI-10-1 this groove is deeper and narrower, as in *P. cancrivorus* (Figure 6a,c).

The deltoid tuberosity (*tuberositas deltoidea*) and pectoral tuberosity are variable in development among specimens of *Cyonasua*. These tuberosities show greater development in FMNH P 14342 and MACN-Pv 2914 compared to other fossil specimens (Figures 4a,c and 5a,e), but not as marked as in *N. nasua*, *N. olivacea*, and *P. flavus*, which present the most developed tuberosities among extant SA procyonids (Figures 4j,k,m and 5g,h,j). However, the development is poor in fossil specimens MLP 04-VI-10-1, MACN-Pv 6689, and MACN-Pv 6688, being similar to that of *P. cancrivorus* and *Bassaricyon* (Figures 4b,e,g,i,l and 5b,c,d,f,i).

The distal humeral epiphysis is preserved in several specimens: MLP 04-VI-10-1, MLP 35-X-4-4, MLP 29-X-8-18, MACN-Pv 2914, FMNH PM 20453, and FMNH P 14342. In general, the condyle (=*trochlea humeri* + *capitulum humeri*) is deep, cylindrical and latero-medially compressed. The capitulum (*capitulum humeri*) and the trochlea (*trochlea humeri*) may be differentiated by the presence of a condyle constriction displaced somewhat laterally. Thus, the capitulum is more expanded respect to the trochlea. The articular surface in FMNH P 14342, MACN-Pv 2914, and MLP 29-X-8-18 is less deep than in other fossil specimens and slightly more latero-medially extended. The humeral trochlea in all specimens of *Cyonasua* is well defined by a medial border that protrudes distally further than the capitulum and somewhat medially oblique. The capitulum is slightly convex with an almost straight distal margin. The articular surface partially resembles that of *P. cancrivorus*; it is narrow, latero-medially compressed, with the humeral trochlea protruding distally and the capitulum presenting a straight distal margin; this latter feature, together with the oblique

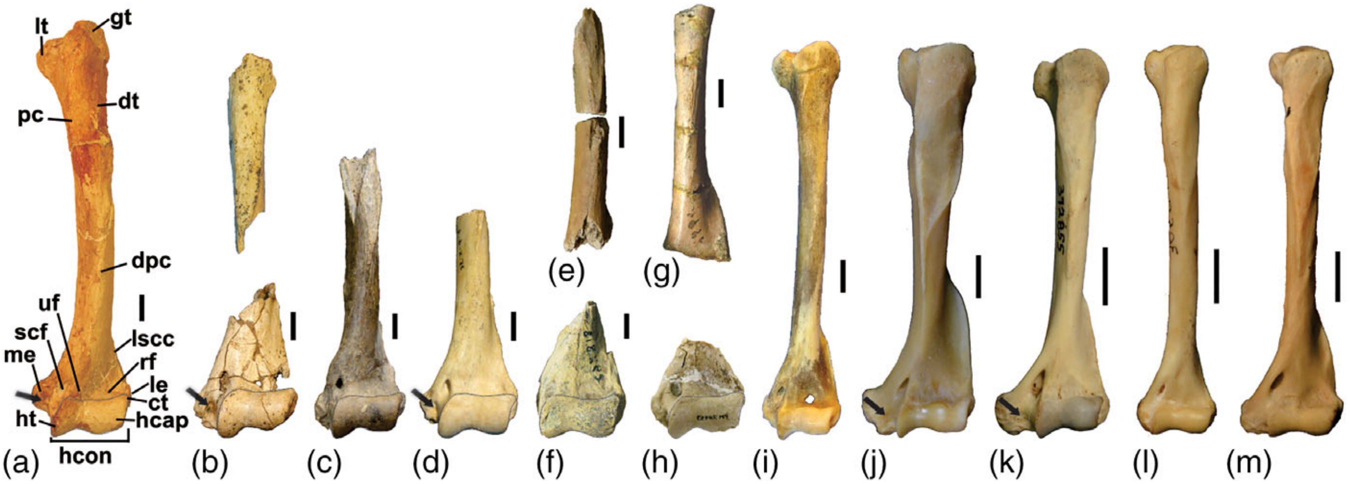

FIGURE 4 Cranial view of the humerus. (a) *Cyonasua* sp. FMNH P 14342, (b) *Cyonasua* sp. MLP 04-VI-10-1, (c) *Cyonasua* sp. MACN-Pv 2914, (d) *Cyonasua* sp. MLP 35-X-4-4 (inv.), (e) *Cyonasua* sp. MACN-Pv 6689 (inv.), (f) *Cyonasua* sp. MLP 29-X-8-18 (inv.), (g) *Cyonasua* sp. MACN-Pv 6688 (inv.), (h) *Cyonasua* sp. FMNH PM 20453 (inv.), (i) *P. cancrivorus* MLP 2110, (j) *N. nasua* MNRJ 79349 (inv.), (k) *N. olivacea* USNM 372855, (l) *B. medius* USNM 305748 (inv.), (m) *P. flavus* AMNH 266597 (inv.). Abbreviations: ct = capitular tail; dpc = deltopectoral crest; dt = deltoid tuberosity; gt = greater tubercle; hcap = humeral capitulum; hcon = humeral condyle; ht = humeral trochlea; le = lateral epicondyle; lscc = lateral supracondylar crest; lt = lesser tubercle; me = medial epicondyle (entepicondyle); pc = pectoral crest; rf = radial fossa; scf = supracondylar foramen; uf = ulnar fossa; black arrow indicates the cranial oval concavity on medial epicondyle; the humeral condyles of fossil specimens are highlighted with a fine black line. Scale bars: 1 cm, specimen (h) has not scale [Color figure can be viewed at wileyonlinelibrary.com]

medial side of the trochlea, also resembles the condition in *N. nasua*. In contrast, in *Potos flavus* and *Bassaricyon* the distal articular surface is shallower (i.e., less extended proximo-distally) and the trochlea is less extended distally, not surpassing the distal margin of the capitulum (Figure 4l,m). *Potos flavus* presents the greatest reduction of the *trochlea* with respect to *capitulum*, and the latter is markedly convex. The morphology of *Nasuella olivacea* is quite particular, with a more latero-medially compressed condyle, a *trochlea* similar to that of fossil procyonids, but marked cylindrical *capitulum* (Figure 4k). In both fossil and extant SA procyonids (except *P. flavus*) the humeral condyle presents a well-defined lateral margin ("capitular tail," sensu Sargis, 2002) particularly evident in *N. olivacea* and *N. nasua* (Figure 4).

Above the distal articular surface, the ulnar fossa (*fossa coronoidea*), is shallow in *Cyonasua* as in *P. cancrivorus*, while it is somewhat deeper in *N. nasua* and *N. olivacea* (Figure 4a-d,f,h,i-k). The ulnar fossa is well developed in *Bassaricyon* and *P. flavus* (Figure 4l,m). The more lateral radial fossa (*fossa radialis*) forms a conspicuous concavity in all specimens of *Cyonasua* except for MLP 04-VI-10-1 in which it is damaged, deeper than in *P. flavus*, *Bassaricyon*, *N. nasua*, and *N. olivacea*, but shallower than in *P. cancrivorus* (Figure 4).

The medial epicondyle (*epicondylus medialis*) of *Cyonasua* is robust and shows moderate to intermediate development compared to extant SA procyonids (Figures 4 and 7). It is oriented posteriorly with respect to the condyle, more so than in any of the other SA procyonids that present some degree of caudal orientation (e.g., *P. cancrivorus*). The medial epicondyle of *Cyonasua* resembles that of *P. cancrivorus*, although slightly more developed that in the latter. The living species *P. flavus*, *N. nasua*, and *N. olivacea* present greater development of the medial epicondyle, whereas *Bassaricyon* presents the least development among SA procyonids (Figures 4 and 7).

Some specimens of *Cyonasua* (MLP 04-VI-10-1 and MLP 35-X-4-4) present a deep oval concavity on the cranial surface of the medial epicondyle; such a condition is observed only in some specimens of *N. nasua* and *N. olivacea* (Figure 4, black arrow). The supracondylar foramen (*foramen supracondylare*) for passage of the median nerve and median artery, is wide and located close to the *trochlea* in *Cyonasua*; whereas in all extant SA procyonids this foramen is more proximal and hence more distant from the *trochlea* (Figure 4). The lateral epicondyle (*epicondylus lateralis*) of both extinct and extant SA procyonids is poorly developed (Figures 4 and 7). The lateral supracondylar crest (*crista supracondylaris lateralis*) is markedly extended proximo-distally in *Cyonasua*, (although particularly short in FMNH P 14342, possibly a bias due to their fragmentary preservation), but not much expanded latero-medially (it is more expanded in MACN-Pv 6688). In general, this crest is similar in size and shape to that of *P. cancrivorus* and *Bassaricyon*, except for MACN-Pv 6688 in which it resembles the condition of *N. nasua*, *N. olivacea*, and *P. flavus* (Figure 4). The olecranon fossa (*fossa olecrani*) in *Cyonasua* is rounded and deeper than in most extant SA procyonids, except for *P. cancrivorus* in which the fossa is perforated forming a supratrochlear foramen (*foramen supratrochleare*; Figure 4).

3.1.3 | Ulna

This element is well preserved in only two specimens: MLP 04-VI-10-1 and MACN-Pv 9968, while only the proximal epiphysis is preserved in MACN-Pv 6689, MACN-Pv 10050, and FMNH P 14342.

The ulna of *Cyonasua* is a robust element in comparison with that of extant SA procyonids, and slightly curved (medially concave). A rough area possibly resulting from pathological origin could be observed on the diaphysis of MLP 04-VI-10-1 (Figure 8Aa,Ba, white arrow). The proximal half of the caudal margin of the ulnar diaphysis is straight to slightly convex, similar to that of *P. cancrivorus*. In contrast, in the remaining SA procyonids the caudal margin of the diaphysis presents

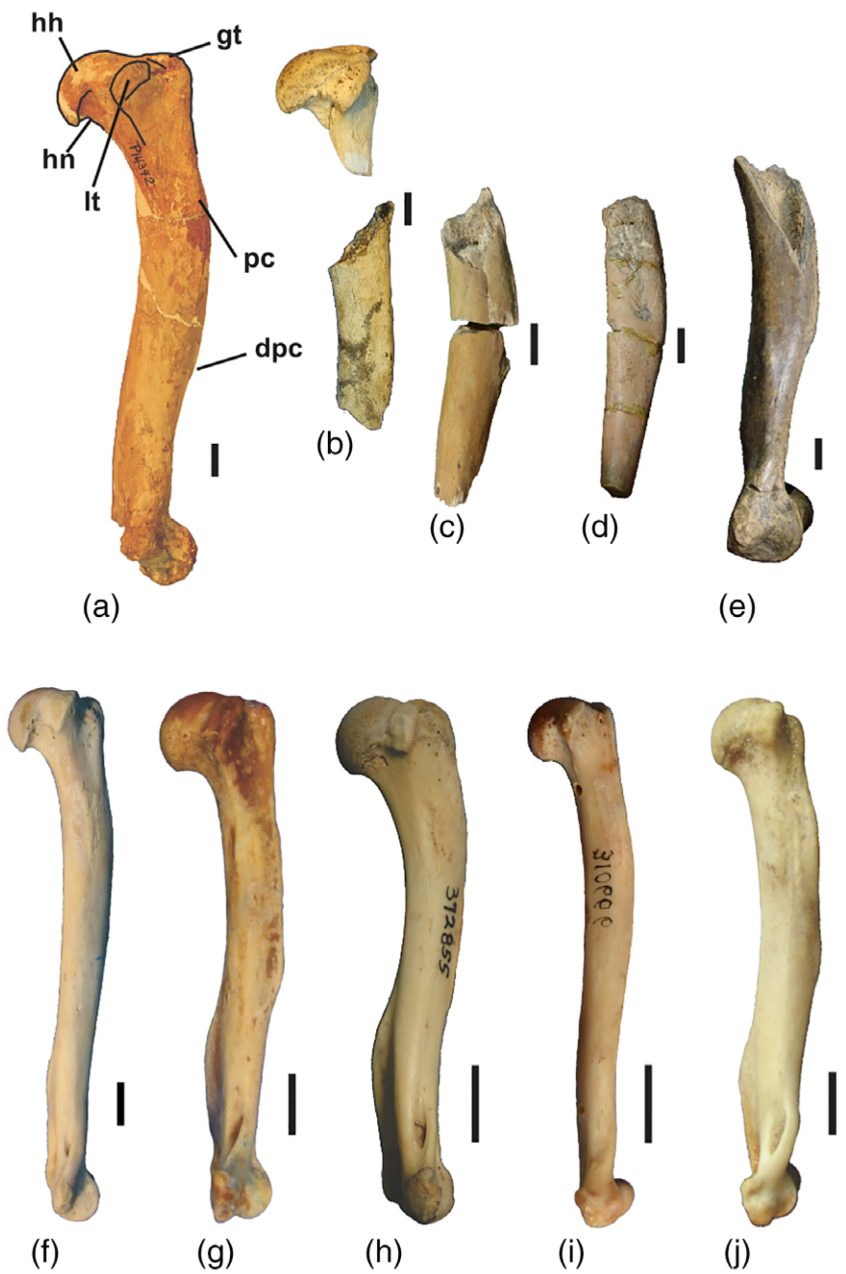

FIGURE 5 Medial view of the humerus. (a) *Cyonasua* sp. FMNH P 14342, (b) *Cyonasua* sp. MLP 04-VI-10-1, (c) *Cyonasua* sp. MACN-Pv 6689 (inv.), (d) *Cyonasua* sp. MACN-Pv 6688 (inv.), (e) *Cyonasua* sp. MACN-Pv 2914, (f) *P. cancrivorus* MNHN 1268 (inv.), (g) *N. nasua* MACN-Ma 33,269 (inv.), (h) *N. olivacea* USNM 372855, (i) *B. medius* USNM 310666 (inv.), (j) *P. flavus* MLP 1740. Abbreviations: hh = humeral head; hn = humeral neck; gt = greater tubercle; lt = lesser tubercle; pc = pectoral crest; dpc = deltopectoral crest; the humeral head of *Cyonasua* sp. FMNH P 14342 is highlighted with a fine black line. Scale bars: 1 cm [Color figure can be viewed at wileyonlinelibrary.com]

diverse degrees of convexity, being more convex in *N. nasua*, *N. olivacea*, and *P. flavus* (Figure 8).

The *olecranon* of *Cyonasua* is relatively robust and straight with respect to the ulnar greater axis, resembling the condition observed in *P. cancrivorus*. In contrast, the *olecranon* of *Bassaricyon* and *P. flavus* is somewhat more proximally elongated, and even more so in *N. nasua* and *N. olivacea* compared to *Cyonasua*. In extant SA procyonids except for *P. cancrivorus* and *N. nasua*, the *olecranon* is directed cranially (Figure 8).

On the medial and proximal aspect of the *olecranon*, *Cyonasua* shows a well-marked fossa whose caudo-proximal margin extends to the medial side forming a wide area for attachment of antebrachial extensor muscles. Among extant SA procyonids, *N. nasua* and *N. olivacea* possess the deepest fossa, *P. cancrivorus* has a moderate one, and *Bassaricyon* and *P. flavus* present a superficial groove. On the lateral side of the diaphysis, caudal to the trochlear notch (*incisura trochlearis*), a deep groove for muscle attachment extends distally. In extant SA procyonids this lateral groove is well developed with some intraspecific variation; it is shallowest in *Bassaricyon* (Figure 8A). The trochlear notch of *Cyonasua* is deep, wide and with a moderately expanded distal margin, resembling those of *P. flavus*, *Bassaricyon*, and *N. nasua* (Figure 8a,d,g,i–m). In contrast, *P. cancrivorus* and *N. olivacea* present a narrower trochlear notch than *Cyonasua*, somewhat shallower in *P. cancrivorus* and deeper in *N. olivacea* (Figure 8f,h).

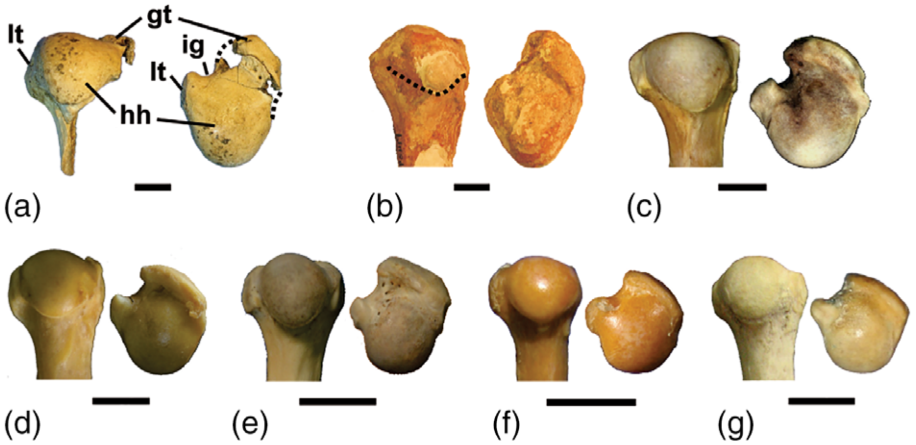

FIGURE 6 Caudal and proximal views of humeral head. (a) *Cyonasua* sp. MLP 04-VI-10-1, (b) *Cyonasua* sp. FMNH P 14342, (c) *P. cancrivorus* MLP 1.I.03.25 (inv.), (d) *N. nasua* MNRJ 79184, (e) *N. olivacea* USNM 372855 (inv.), (f) *B. gabbii* AMNH 184985, (g) *P. flavus* MLP 1740. Abbreviations: gt = greater tubercle; hh = humeral head; ig = intertubercular groove; lt = lesser tubercle; dotted lines indicate the anatomical reconstruction. Scale bars: 1 cm [Color figure can be viewed at wileyonlinelibrary.com]

The radial notch (*incisura radialis*) of the ulna for articulation with the radius is relatively narrow in *Cyonasua* and surpasses the distal edge of the trochlear notch, similarly to the condition observed in *P. cancrivorus* (Figures 8 and 9). Although this structure does not exhibit marked differences among extant SA procyonids, *N. nasua*, *N. olivacea*, *Bassaricyon*, and *P. flavus* present a wide radial notch with notable distal extension respect to the distal margin of the trochlear notch; these features are more evident in the two latter taxa (Figure 9i,j).

The *processus anconeus* of *Cyonasua* is convex, prominent and well developed, with its lateral side more enlarged proximally than the medial one. This feature presents some variation among extant SA procyonids: the *processus anconeus* of *P. cancrivorus* resembles that of *Cyonasua*; however, *P. flavus* and *Bassaricyon* present a latero-medially wide and slightly convex *processus*, with both surfaces almost equally projected. In *N. olivacea* the medial surface of the *processus anconeus* is slightly more extended than the lateral one, and in *N. nasua* it is convex, with both surfaces equally extended proximally (Figure 9).

On the distal end of the ulnar diaphysis, a medial crest demarcates a large and flat anterior area for attachment of *m. pronator quadratus*. The markedly distal position and the degree of development of this crest in *Cyonasua*, resembles the condition of *N. nasua* and *N. olivacea*

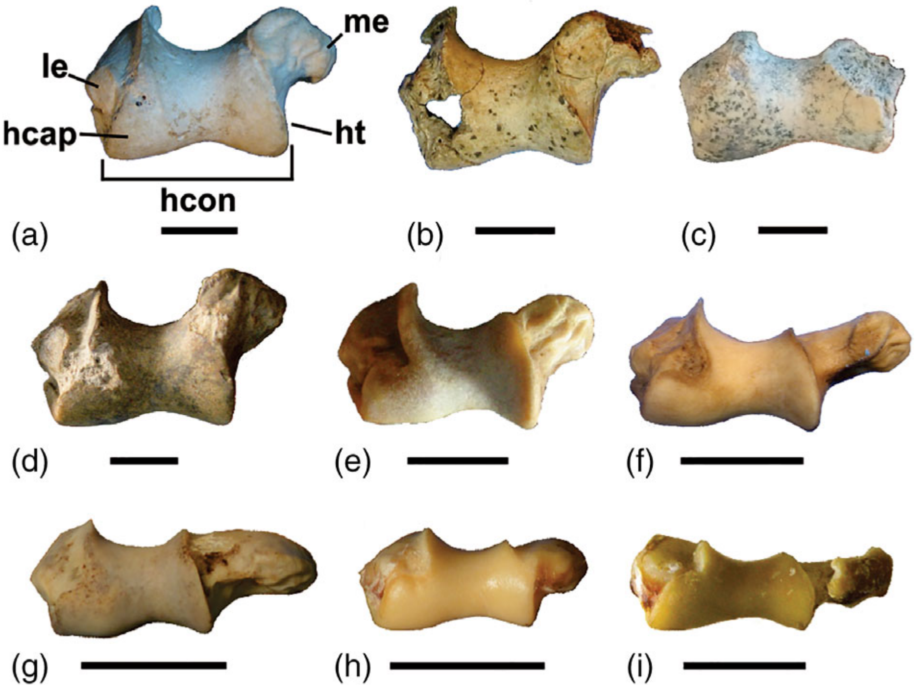

FIGURE 7 Distal views of the humerus. (a) *Cyonasua* sp. MLP 35-X-4-4 (inv.), (b) *Cyonasua* sp. MLP 04-VI-10-1, (c) *Cyonasua* sp. MLP 29-X-8-18 (inv.), (d) *Cyonasua* sp. MACN-Pv 2914, (e) *P. cancrivorus* MLP 1.I.03.25, (f) *N. nasua* MACN-Ma 25862, (g) *N. olivacea* USNM 372855, (h) *B. medius* USNM 305748 (inv.), (i) *P. flavus* MNRJ 68610 (inv.). Abbreviations: hcap = humeral capitulum; hcon = humeral condyle; ht = humeral trochlea; le = lateral epicondyle; me = medial epicondyle (entepicondyle). Scale bars: 1 cm [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 8 Ulna. (A) Lateral view, (B) medial view, (a) *Cyonasua* sp. MLP 04-VI-10-1, (b) *Cyonasua* sp. MACN-Pv 9968 (inv.), (c) *Cyonasua* sp. FMNH P 14342 (inv.), (d) *Cyonasua* sp. MACN-Pv 6,689 (inv.), (e) *Cyonasua* sp. MACN-Pv 10050 (inv.), (f) *P. cancrivorus* MLP 1.I.03.25 (inv.), (g) *N. nasua* MNRJ 79184 (inv.), (h) *N. olivacea* FMNH 70745, (i) *B. gabbii* AMNH 184985, (j) *B. medius* USNM 305748 (inv.), (k) *B. neblina* USNM 598996 (inv.), (l) *B. alleni* USNM 395837 (inv.), (m) *P. flavus* MLP 1470 (inv.). Abbreviations: Ca = *circumferentia articularis*; lg = lateral groove of ulnar diaphysis; ol = *olecranon*; pa = *processus anconeus*; rn = radial notch; spu = styloid process of the ulna; tn = trochlea notch; black line indicates medial crest for attachment of *M. pronator quadratus*; white arrow indicates pathological process. Scale bars: 1 cm [Color figure can be viewed at wileyonlinelibrary.com]

rather than that of *P. flavus* and *Bassaricyon*, because in these latter taxa the crest does not extend much proximally. However, in *P. cancrivorus* the medial crest is less developed and located slightly more proximally (Figure 8B).

The distal ulnar epiphysis is completely preserved only in one specimen (MLP 04-VI-10-1). It presents a robust styloid process (*processus styloideus*), with a short neck and located posteriorly with respect to the diaphyseal axis (Figure 8). This posterior location is observed in most extant SA procyonids except for *P. flavus* and *N. olivacea*, in which this process is placed following approximately the ulnar sagittal axis. In *P. cancrivorus*, the styloid process of the ulna is elongated and relatively graceful, in *Bassaricyon* it is strong and moderately elongated, while it is short in *N. nasua* and *N. olivacea*. The distal articular facet for the radius (*circumferentia articularis*) of *Cyonasua* sp. is robust and projected cranially, as in most extant SA procyonids; this condition is more marked in *P. flavus* and some species of *Bassaricyon* (e.g., *B. alleni*, *B. gabbii*), while this facet is shallow in *P. cancrivorus* (Figure 8).

3.1.4 | Radius

The radius is preserved, although fragmentarily, in MLP 04-VI-10-1, MACN-Pv 6689, and FMNH P 14342. The radial head (*caput radii*) preserved in MACN-Pv 6689 has an ovoid outline that resembles that of *P. cancrivorus* in terms of its maximum length (latero-medial distance). Among extant SA procyonids, *P. flavus* and *B. neblina* have the lower maximum length of the radial head; in contrast, *N. nasua*, *N. olivacea*, *B. alleni*, *B. medius*, and *B. gabbii* have the highest maximum length of the radial head among extant and fossil procyonids analyzed (Figure 10). The cranial margin of the radial head in *Cyonasua* shows a protuberance that is present in most extant SA procyonids, and especially marked in *N. nasua* and *N. olivacea* (Figure 10). The proximal surface of the radial head for articulation with the *capitulum humeri* (*fovea capitis radii*) is slightly concave in *Cyonasua*, similarly to that of *P. cancrivorus* and *N. nasua*, whereas it is more concave in *Bassaricyon* and *P. flavus*.

The radius of MACN-Pv 6689 and FMNH P 14342 suggest some degree of diaphysal curvature, at least slightly greater than in *P. cancrivorus* (Figures 10 and 11). In almost all extant SA procyonids, the cranial and lateral aspect of the radial diaphysis are curved, creating a convex surface; however, the radial diaphysis of *P. cancrivorus* is mostly straight (Figures 10 and 11). The diaphyses of FMNH P 14342 and MLP 04-VI-10-1 are robust, antero-posteriorly depressed as in *P. cancrivorus*. In posterior view, the radial diaphysis of *Cyonasua* presents a conspicuous and well-developed crest that extends along its middle surface parallel to the sagittal plane, slightly directed medially (more medially located in MLP 04-VI-10-1 than in FMNH P 14342) and delimiting medially a narrow area for attachment of *m. pronator quadratus* (Figure 10). Thus, at that level the diaphysis is triangular in cross section. Among extant SA procyonids, the condition in *P. cancrivorus* is similar to *Cyonasua*; whereas, in *N. nasua*, *N. olivacea*, *P. flavus*, and *Bassaricyon*, the caudal surface of the diaphysis is markedly broad for muscle attachment (Figure 10).

The radius of MLP 04-VI-10-1 presents, at about mid-diaphysis, an irregular and rough overgrowth of bone that clearly denotes a pathological process (Figure 10, white arrow). A similar condition is evident in the ulna of the same specimen (see above).

The distal epiphysis (*trochlea radii*) of *Cyonasua* sp. is robust; the styloid process (*processus styloideus*) is more extended distally than in extant SA procyonids, pointed in anterior view and semicircular in medial view, with a triangular outline. Even though it is most similar to that of *P. cancrivorus*, in the latter the styloid process is slightly sharper. In contrast, in the other extant SA procyonids this process is well-developed but less sharp (*N. nasua*, *N. olivacea*) or blunt (*P. flavus*, *Bassaricyon*; Figure 10).

The distal carpal surface for articulation with the *scapholunatum* (*facies articularis carpea*) has been preserved in MLP 04-VI-10-1. It is similar to that of *P. cancrivorus*, with a latero-medially wide, and slightly concave surface extending medially over the lateral aspect of the *processus styloideus*, and subquadrangular in shape; the articular plane is perpendicular to the sagittal plane (see dotted line in Figure 10c,d). Conversely, among other extant SA procyonids, the distal carpal surface is slightly more extended antero-posteriorly and presents an oval outline (especially more oval in *Potos flavus*), and its articular plane is inclined medially with respect to the sagittal plane (Figure 10e–h).

The ulnar notch (*incisura ulnaris*) of MLP 04-VI-10-1 is small, oval and does not contact the scapholunar facet. This is similar to the condition observed in *P. cancrivorus*, whereas in the other extant SA procyonids the ulnar notch is larger. In particular, in *Potos flavus* and *Bassaricyon* this facet is located more distally, nearly contacting the distal carpal surface (Figure 11).

On the cranial-medial surface of the distal epiphysis of MLP 04-VI-10-1 there are deep furrows delimited by crests for the passage

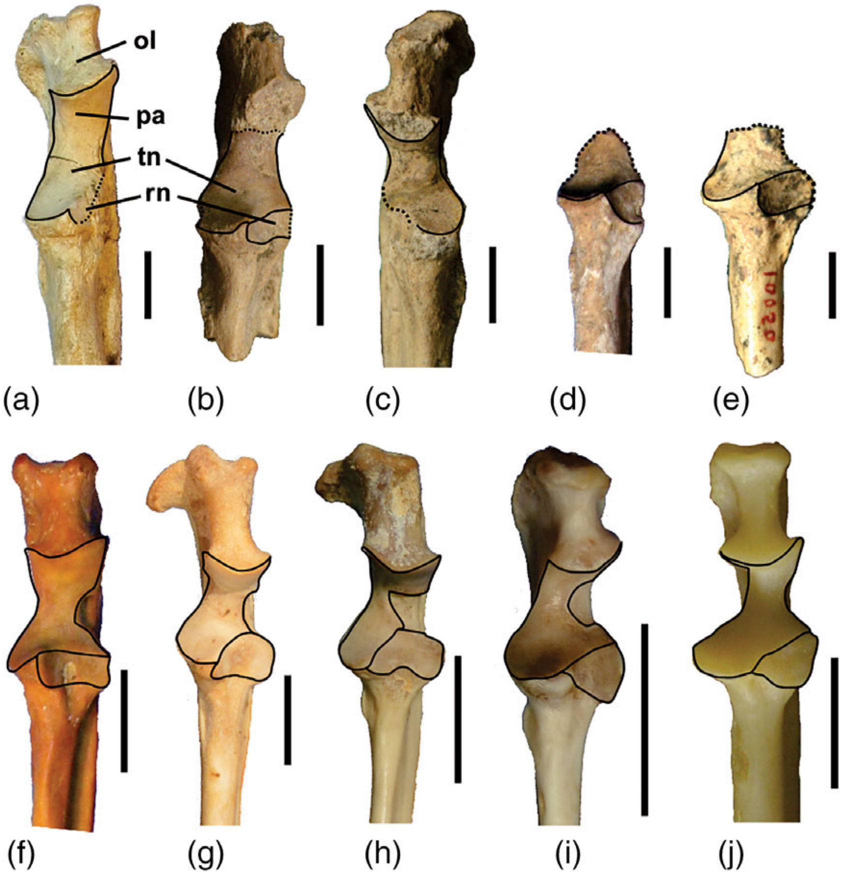

FIGURE 9 Cranial view of proximal portion of the ulna. (a) *Cyonasua* sp. MLP 04-VI-10-1, (b) *Cyonasua* sp. MACN-Pv 6689 (left ulna), (c) *Cyonasua* sp. MACN-Pv 6689 (right ulna), (d) *Cyonasua* sp. MACN-Pv 9968, (e) *Cyonasua* sp. MACN-Pv 10050 (inv.), (f) *P. cancrivorus* MNHN 2714 (inv.), (g) *N. nasua* AMNH 134007 (inv.), (h) *N. olivacea* USNM 372855, (i) *B. alleni* USNM 396992 (inv.), (j) *P. flavus* MNRJ 55500 (inv.). Abbreviations: ol = *olecranon*; pa = *processus anconeus*; rn = radial notch; tn = trochlea notch; the structure of the articular surface is highlighted with a black line and broken portions are outlined with dotted lined. Scale bars: 1 cm [Color figure can be viewed at wileyonlinelibrary.com]

of tendons of extensor and abductor muscles of the autopodium (Figure 11g–l). In *P. cancrivorus*, *N. nasua*, and *N. olivacea*, these crests are well developed, somewhat more than in MLP 04-VI-10-1, whereas in the other extant SA procyonids they are low but delimit wider furrows.

3.2 | Anterior autopodium

Few elements of the anterior autopodium of fossil SA procyonids are known, all of them correspond to specimen MLP 04-VI-10-1 (*Cyonasua* sp.; Figure 12A).

The left pisiform (*carpi accessorium*, *pisiforme*) preserved is cylindrical to prismatic-triangular, with a dorsoventrally compressed neck (middle portion), triangular in cross-section and latero-medially wide (Figure 12Aa). The proximal end presents two smooth, slightly concave facets contacting each other medially. The postero-lateral facet, which articulates with the ulna, is drop-shaped, whereas the antero-medial facet, which articulates with the ulnar carpal bone (*carpi ulnare*, *triquetrum*), is kidney-shaped. The pisiform of *Cyonasua* sp. differs from that of *P. cancrivorus* by being more robust and having a ventrally projected facet for articulation with the ulnar carpal bone. This latter feature is also observed in *N. nasua*. Conversely, the free distal ends of the pisiform are quite expanded antero-posteriorly and notably developed compared with *N. nasua* and *P. cancrivorus*; the margins of the distal end are irregular and expanded, with an oblique crest separating two areas for muscle attachment (Figure 12Ba,Ca).

The morphology of the third carpal bone (*carpale III*, *capitatum*, *magnum*) is relatively conservative among extant SA procyonids, with some variation in robustness (Figure 12Ab,Bb,Cc). This element is larger in *Cyonasua* sp. than in extant SA procyonids (Figure 12A–F). In dorsal view, its proximal portion is lateromedially compressed, while in lateral view it presents a semicircular shape. Its proximal surface, for articulation with the scapholunar (*scapholunatum*), is convex and smooth. On its medial aspect it presents a narrow articular surface for the second carpal (*carpale II*, *trapezoideum*) and below this, a fossa with roughened surface, possibly for attachment of an interosseus ligament. Laterally it presents a crescent-shaped facet for the fourth carpal (*carpale IV*, *hamatum*) and ventral to this facet, a deep rough fossa for the interosseus ligament. Distally, the articular facet for the third metacarpal is wide and presents a concave articular surface, dorso-ventrally elongated, almost rectangular in outline, and with the dorsal margin more extended than the ventral one (Figure 12Ab). In *N. nasua*, the distal articular facet is relatively wide but more concave; whereas it is narrower and slightly more concave in *P. cancrivorus* than in *Cyonasua* sp. (Figure 12Bb,Cc). The plantar surface of the third carpal of *Cyonasua* sp. is rough, convex and presents a tuberosity slightly larger than that of *N. nasua*, but larger than that of *P. cancrivorus* (Figure 12Ab,Bb,Cb).

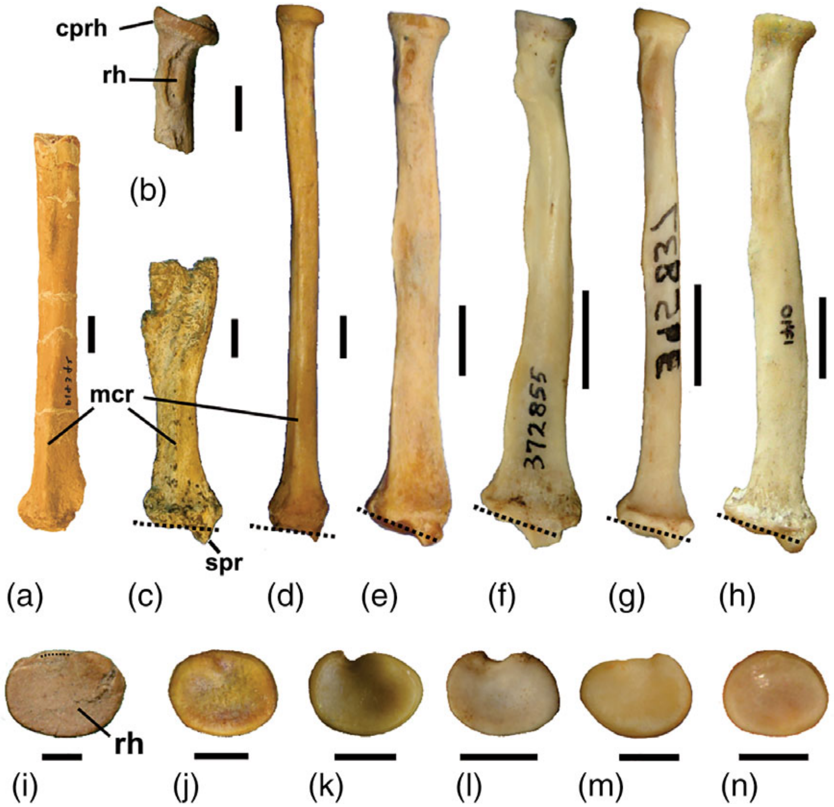

FIGURE 10 Caudal and proximal views of the radius. (a–h), caudal view of the radius, (i–n) proximal view of radial head. (a) *Cyonasua* sp. FMNH P 14342, (b,i) *Cyonasua* sp. MACN-Pv 6689, (c) *Cyonasua* sp. MLP 04-VI-10-1, (d) *P. cancrivorus* MACN-Ma 32254 (inv.), (e) *N. nasua* MACN-Ma 33269 (inv.), (f,l) *N. olivacea* USNM 372855, (g,m) *B. alleni* USNM 395837 (inv.), (h) *P. flavus* MLP 1470 (inv.), (j) *P. cancrivorus* MNRJ 5503, (k) *N. nasua* MNRJ 79184, (n) *P. flavus* AMNH 267607. Abbreviations: cprh = cranial protuberance of the radial head; mcr = medial crest; rh = radial head; spr = styloid process of the radius, dotted straight line indicates the position of the articular plane. Scale bars: (a–h): 1 cm, (i–n): 0.5 cm [Color figure can be viewed at wileyonlinelibrary.com]

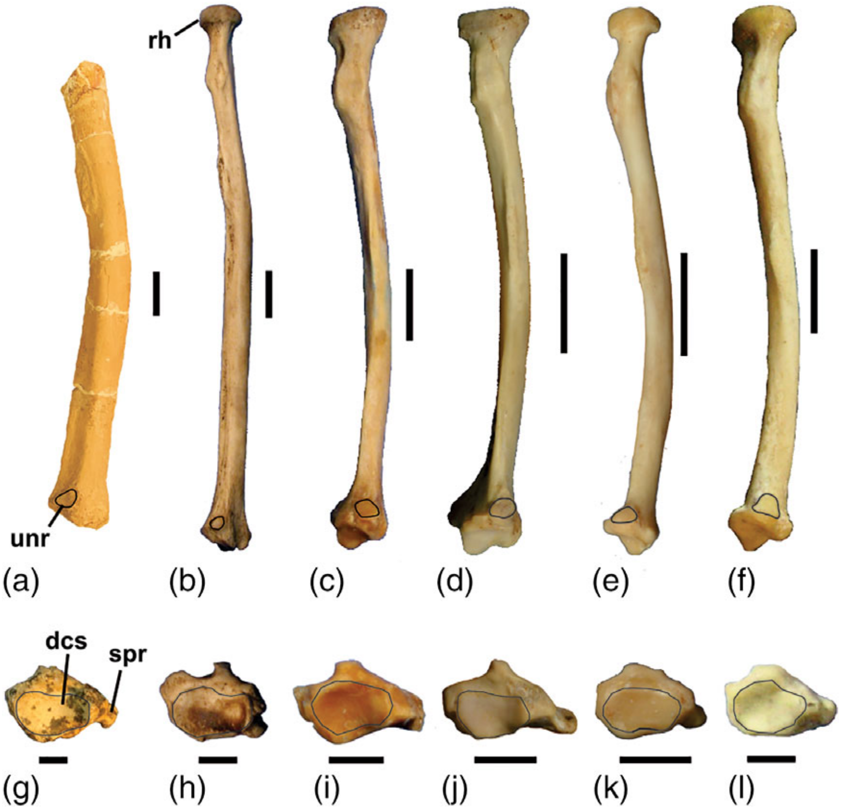

FIGURE 11 Lateral and distal views of the radius. (a–f) lateral view of the radius, (g–l) distal view of distal epiphysis. (a) *Cyonasua* sp. FMNH P 14342, (b,h) *P. cancrivorus* MNHN 3285, (c,i) *N. nasua* MACN-Ma 33.269, (d,j) *N. olivacea* USNM 372855 (inv.), (e,k) *B. alleni* USNM 395837, (f,l) *P. flavus* MLP 1740, (g) *Cyonasua* sp. MLP 04-VI-10-1. Abbreviations: dcs = distal carpal surface, highlight with fine black line; rh = radial head; spr = styloid process of the radius; unr = ulnar notch of the radius, highlighted with a fine black line. Scale bars: (a–f): 1 cm, (g–l): 0.5 cm [Color figure can be viewed at wileyonlinelibrary.com]

3.2.1 | Metacarpals and phalanges

Only the right first metacarpal of the specimen MLP 04-VI-10-1 has been preserved (Figure 12Ac). It is shorter and more robust compared to the gracile morphology found in extant SA procyonids. Among living SA procyonids, the first metacarpal is more robust in *N. nasua* and *N. olivacea* (Figure 12Cc,D) than in other taxa, resembling the morphology of *Cyonasua* sp. In contrast, the first metacarpal of *P. cancrivorus*, *P. flavus*, and *Bassaricyon* is gracile and elongated (Figure 12Bc,E,F). The proximal epiphysis of the first metacarpal of MLP 04-VI-10-1 is larger than the distal epiphysis. The proximal facet for the first carpal bone (*trapezium*) is rectangular, medially oblique, convex and smooth (Figure 12Ac). On the latero-proximal side, it bears a well-developed, oval proximal facet similar to that of *P. flavus* and *N. nasua*; this facet is slightly less developed in *P. cancrivorus* (Figure 12Bc,Cc,E). In medial view, it presents an ovoid concavity that would correspond to the articular surface for metacarpal II (Figure 12c). The diaphysis of the first metacarpal bears a ventral crest at midshaft, more developed than in extant SA procyonids. In dorsal view, near its distal end (*caput*), the first metacarpal presents irregular shape and some protuberances in dorsal view. In contrast, this dorsal surface is smooth in extant SA procyonids. On its distal end, it bears a rounded (slightly globular shape) and narrow condyle (*caput*) for articulation with the first phalanx. The medial and lateral margins of the condyle are straight and oblique, respectively. Ventrally, the condyle of *Cyonasua* sp. presents a conspicuous protuberance, it is slightly more developed than that of *N. nasua* and even more than that of *P. cancrivorus* (Figure 12Ac,Bc,Cc).

Only two proximal phalanges of the specimen MLP 04-VI-10-1 have been preserved, possibly corresponding to the hand according to their morphology and size (Figure 12Ad,e). They are thick and short in comparison with extant SA procyonids, in which these elements are more elongated and slender (Figure 12Bd,e;Cd,e). As for first metacarpal morphology, the phalanges of *Cyonasua* sp. resemble those of the extant SA procyonids *N. nasua* and *N. olivacea*, although as stated above, they are somewhat more robust (i.e., relatively short and wide) than those of the latter two species (Figure 12Bd,e;Cd,e). In lateral and medial view, the phalangeal diaphyses of *Cyonasua* sp. are curved (convex dorsally), proximally thick but becoming slenderer distally (Figure 12Ad,e). The proximal articular facet is kidney-shaped (major axis of the facet in latero-medial direction), dorso-ventrally flattened and concave, similar to that of *N. nasua* and *P. cancrivorus.* The ventral surface of the smaller phalanx presents small condyles for metatarsal articulation with a flat surface and an incipient intercondylar fossa (Figure 12Ad). This condition resembles the morphology of the proximal phalanges of the first digit of *P. cancrivorus* and *N. nasua* (Figure 12 Bd,Cd). In dorsal view, the distal epiphysis of this smaller phalanx is almost circular in outline, with a lateral concavity on each side. The distal epiphysis of the other phalanx presents a distal concavity (Figure 12Ae).

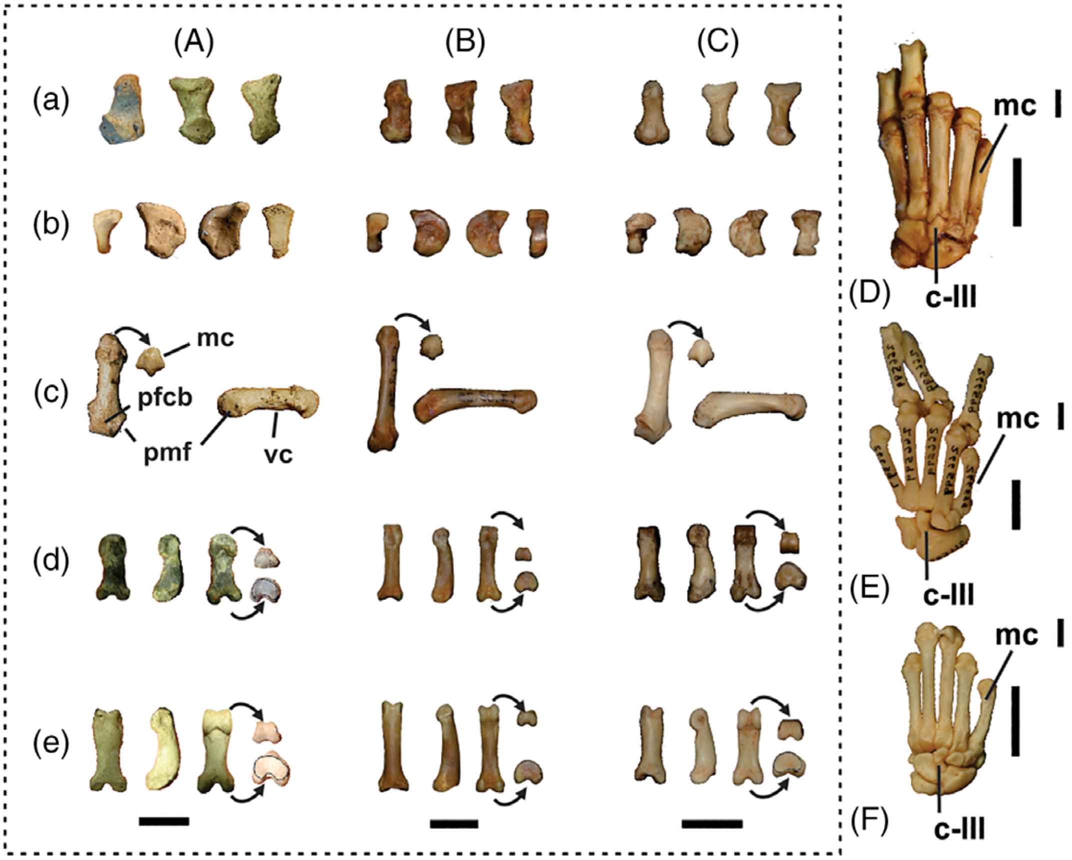

FIGURE 12 Autopodium elements. (A,a-e) *Cyonasua* sp. MLP 04-VI-10-1, (B,a-e) *P. cancrivorus* MLP 1.I.03.25, (C,a-e) *N. nasua* MLP 2550, (D) *N. olivacea* FMNH 70741, (E) *B. alleni* USNM 395837 (inv.), (F) *P. flavus* AMNH 266599 (inv.), (a) pisiform in dorsal, caudal and cranial views, (b) third carpal bone, dorsal, lateral, medial, and distal views, (c) first metacarpal in dorsal, distal, and medial views, (d) proximal phalange of first digit in dorsal, lateral, ventral, distal, and proximal views, (e) phalange of second to five digits in dorsal, lateral, ventral, distal, and proximal views. Abbreviations: c-III = third carpal bone; mc = metacarpal caput; mc I = first metacarpal; pfcb = proximal facet for the first carpal bone; pmf = proximal medial facet, vc = ventral crest. Scale bars: 1 cm [Color figure can be viewed at wileyonlinelibrary.com]

3.3 | Functional indexes

The Humeral Robustness Index (HRI) showed that the average value obtained for the fossil specimen FMNH P 14342 (*Cyonasua* sp.) was relatively high, similarly to those obtained for *Nasua* and *Nasuella* (Figure 13a, Supporting Information Table S3), that are the highest among procyonids; whereas only few taxa of other carnivoran groups presented higher values (e.g., *Conepatus*, *Meles*, *Lontra*, *Melursus*, and *Tremarctos*). With respect to the SP and LM categories, the value for specimen FMNH P 14342 was intermediate to high (Figure 13b, Supporting Information Table S3). This value was close to, although slightly higher, than the mean value for scansorial taxa. In contrast, the mean values for most other categories (i.e., terrestrial-climber, tree-dweller, terrestrial-generalist and terrestrial-cursorial), were below those of FMNH P 14342. Conversely, the semiaquatic category showed the highest values of the sample. With respect to SU categories, FMNH P 14342 obtained HRI values close to the mean values of specialized-digger (Figure 13c). Concerning the influence of size, this was the only index that showed significant correlation with body mass ($p < 0.05$), hence showing positive allometry (Supporting Information Table S4). However, the determination coefficient was low, that is, 30% of the overall variation were explained by differences in body mass.

Regarding the Humeral Distal End Width Index (HDEWI), the specimen FMNH P 14342 showed intermediate value with respect to other procyonids and carnivorans, indicating an intermediate entepicondyle development. The value for *Cyonasua* sp. was close to the mean values for *Arctictis binturong*, *Nandinia binotata*, *Paradoxurus hermaphrodites*, and *Lyncodon patagonicus* (Figure 14a, Supporting Information Table S3). With respect to SP and LM, FMNH P 14342 showed intermediate values similar to most categories, while only semiaquatic and terrestrial-cursorial categories showed extremes (highest and lowest values, respectively; Figure 14b, Supporting Information Table S3). The result for SU showed higher mean value for the specialized digger category, compared to lower mean values for non-specialized/No digger (Figure 14c). *Cyonasua* sp. obtained an intermediate value between the two US categories. This index showed no significant correlation with body size, hence its variation was not affected by allometry (Supporting Information Table S4).The Humeral Condyle Depth Index (HCDI) was analyzed for three fossil specimens (MLP 04-VI-10-1, MLP 35-X-4-4, MACN-Pv 2914) that showed similar values. Their HCDI values were lowest among procyonids and most other specimens of the sample (except for canids, which presented the lowest values), and close to the mean for *Meles meles*. HCDI values varied among procyonids, indicating deepest condyles for fossils procyonids and increasing values, in order, for *Procyon*,

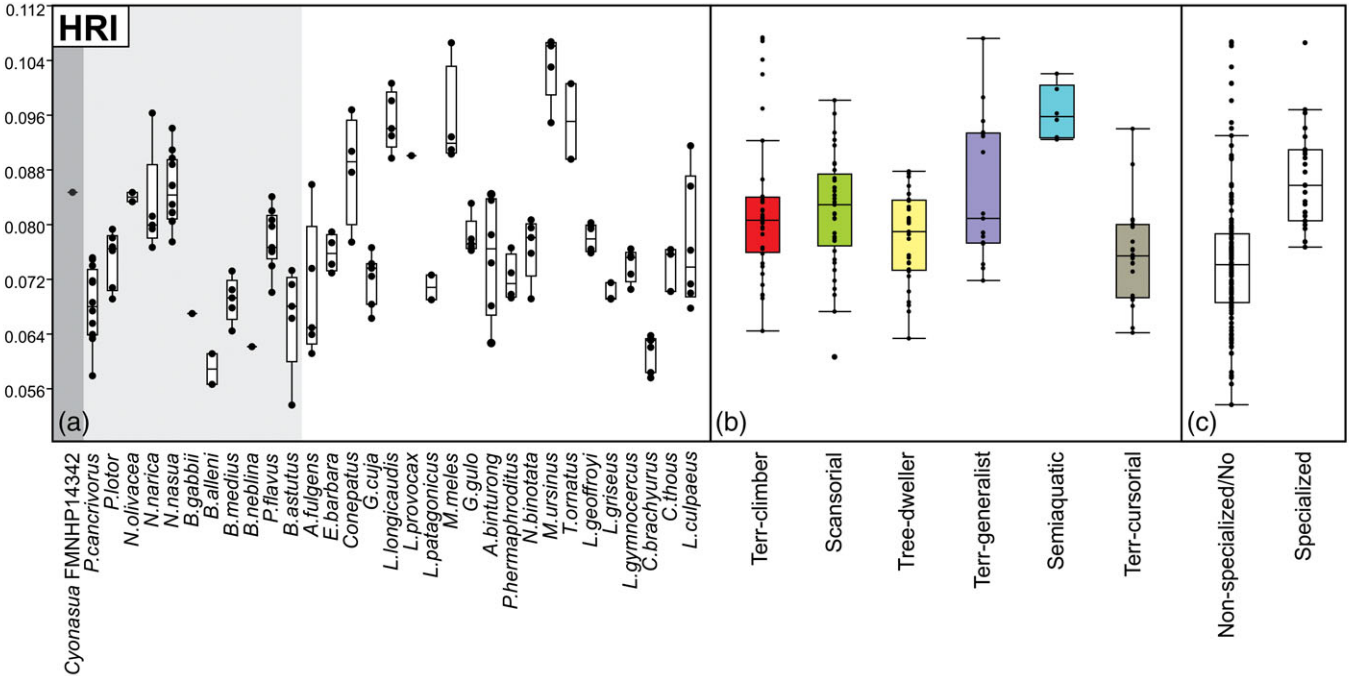

FIGURE 13 Boxplot of humerus robustness index (HRI). The box represents the first and third quartiles; the median is shown by a horizontal line inside the box; short horizontal lines ("whiskers") represent data within 1.5 times the interquartile range. (a) by taxon, (b) by substrate preferences and locomotor mode, (c) by substrate use [Color figure can be viewed at wileyonlinelibrary.com]

Nasuella, *Nasua*, *Bassariscus*, *Bassaricyon*, and finally *Potos* (Figure 15a, Supporting Information Table S3). With respect to SP and LM, *Cyonasua* showed lower values than most categories, except for the terrestrial-cursorial, which included all canids (Figure 15b, Supporting Information Table S3). With respect to SU, the results showed no differences between the two categories analyzed (Figure 15c). This index showed no significant correlation with body size (Supporting Information Table S4).

Regarding the Fossorial index (IFA), the fossil specimen MLP 04-VI-10-1 showed relatively high values among procyonids, closest to those of *Nasua*. This latter genus and *Nasuella* presented the highest values along with *Lontra*, *Conepatus*, *Galictis*, *Meles*, and *Lyncodon*. With respect to others carnivorans, MLP 04-VI-10-1 showed values similar to those obtained for *Paradoxurus hermaphroditus*, *Arctictis binturong*, *Nandinia binotata* and also close to *Melursus ursinus*. (Figure 16a, Supporting Information Table S3). Compared to the analysis of IFA for SP and LM categories, the terrestrial-cursorial taxa showed lowest IFA values, followed in increasing order by terrestrial-climber, tree-dweller, scansorial, terrestrial-generalist, and semiaquatic, the latter with highest values. Specimen MLP 04-VI-10-1 showed values in the range of those obtained for scansorial (Figure 16b, Supporting Information Table S3) and intermediate between SU categories, although in the range of non-specialized/No digger (Figure 16c).

A regression of IFA on Body mass was not significant, indicating that allometry was negligible as a factor on variation.

4 | DISCUSSION

Appendicular morphology is functional relevant in Carnivora, as in other mammals, because of its relationship with diverse functions and behaviors (e.g., locomotion, feeding, grooming, prey-catching and mating). The morphology of the appendicular skeleton is also influenced by other factors, such as body size (Andersson, 2004b; Fabre, Cornette, Peigné, & Goswami, 2013; Iwaniuk, Pellis, & Whishaw, 1999; Polly, 2007) and shared evolutionary history (Felsenstein, 1985; Losos & Miles, 1994).

4.1 | Functional morphology of the pectoral girdle

The pectoral girdle plays an important role in locomotion, especially regarding functional requirements for stabilization of the gleno-humeral joint, and scapular mobility (Fischer, Schilling, Schmidt, Haarhaus, & Witte, 2002). The lack of a well-preserved scapula of *Cyonasua* precludes knowledge of its complete outline. Nevertheless, other features such as the neck extension and the shape of the distal dorsal border seem to indicate a shape from rectangular, as seen in *N. nasua*, to slightly rounded, as in *P. cancrivorus*.

The presence of a well-developed scapular spine in *Cyonasua*, most conspicuous among extant SA procyonids, would reflect an extensive *m. trapezius* and possibly a strong *m. deltoideus* for scapular rotation during locomotion. Most of these characteristics have been associated by different authors (e.g., Janis & Figueirido, 2014; Maynard-Smith & Savage, 1956) with cursorial locomotion, adapted to velocity. However, the strong development of the scapular spine, together with a strong *acromion* with cranially oriented *processus hamatus* and good development of the deltoid crest, indicate that the *m. deltoideus* might have favored both humeral protrusion and abduction, as in other mammals (Argot, 2001; McEvoy, 1982; Sargis, 2002; Taylor, 1974). Similar characteristics were observed in the extant SA procyonids *N. nasua*, *N. nasuella*, *P. flavus*, and *B. medius*, in agreement with the function of these muscles when climbing vertically, when the

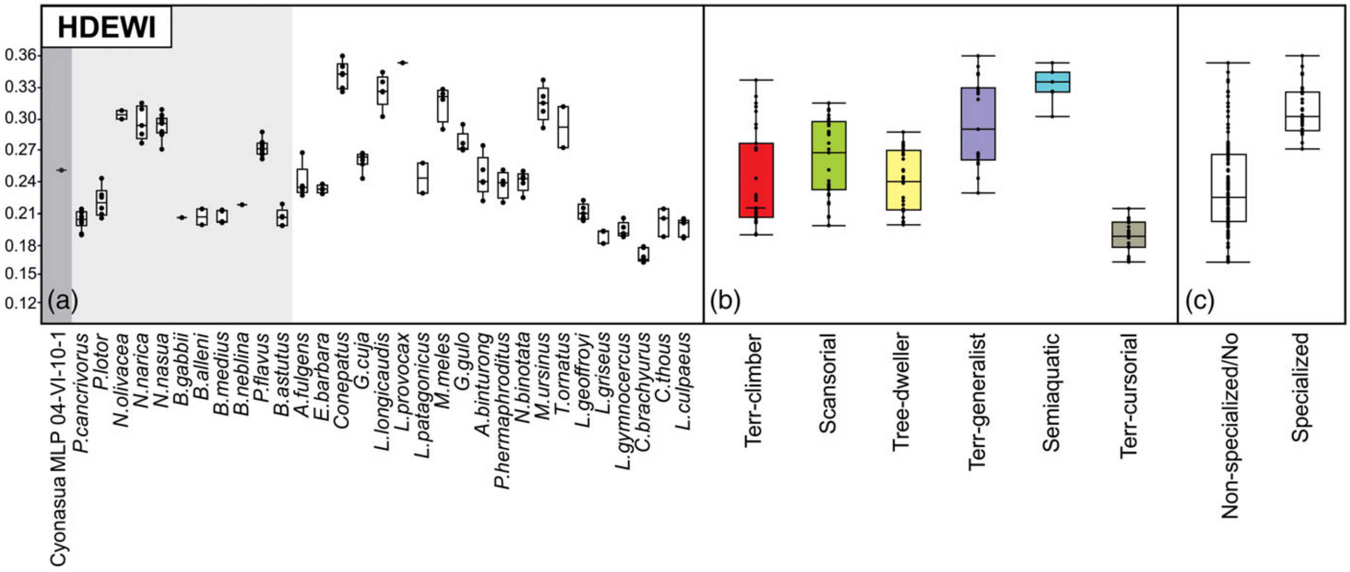

FIGURE 14 Boxplot of humeral distal end width index (HDEWI). For explanation, see Figure 13. (a) by taxon, (b) by substrate preferences and locomotor mode, (c) by substrate use [Color figure can be viewed at wileyonlinelibrary.com]

limbs surround the substrate at the end of stance phase and during propulsion, and the flexor muscles of the shoulder resist and advance the body weight (Argot, 2001; Cartmill, 1985).

Cyonasua shows particular traits in the gleno-humeral joint that differ from extant SA procyonids, but resemble other terrestrial mammals (Evans & de Lahunta, 2013; Sargis, 2002; Taylor, 1974). The features analyzed in both tubercles of *Cyonasua* indicate a gleno-humeral joint more stabilized than that of extant SA procyonids, which would prevent collapse of the joint, increasing the lever arm for *m. supraspinatus*, which favors movements in the parasagittal plane, and a short lever arm of *m. subscapularis* for humeral adduction.

The glenoid cavity and humeral head of *Cyonasua* also show particular characteristics and similarities to those of cursorial mammals (see, Argot, 2001; Argot & Babot, 2011; Gebo & Sargis, 1994; Sargis, 2002; Taylor, 1974; Wang, 1993), and indicate forelimb movements restricted to the parasagittal plane during flexion-extension. In addition, the extended supraglenoid tubercle of *Cyonasua* would have represented an osseous obstacle, acting as a stop for shoulder hyperextension, which in turn helps to prevent possible dislocation of the gleno-humeral joint, especially when the forelimb is in flexed position. This feature has been observed in mammals that have a limited amount of scapular rotation (Roberts, 1974), indicating a stable joint and possibly suggesting that the gleno-humeral joint was subjected to high mechanical stresses in flexed stances, as observed for fossil sloths by Toledo et al. (2012). In contrast, extant SA procyonids show other characteristics that are associated with a wide range of rotational movements in all directions, similar to the condition observed in some living didelphids by Argot (2001).

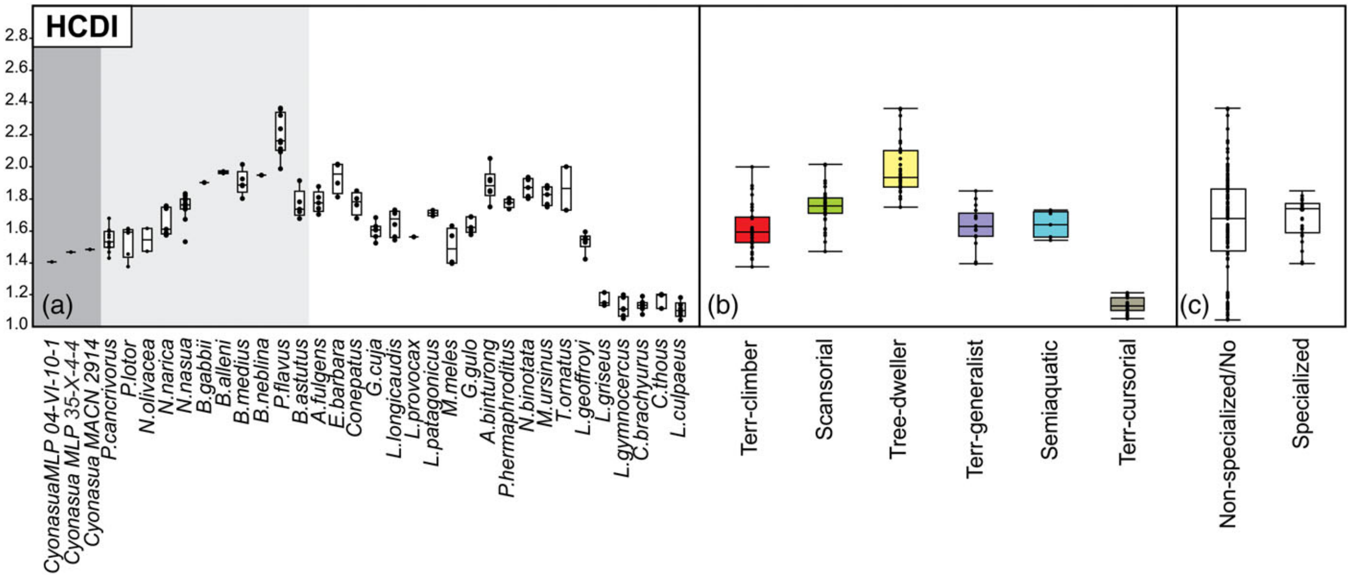

FIGURE 15 Boxplot of humeral condyle depth index (HCDI). For explanation, see Figure 13. (a) by taxon, (b) by substrate preferences and locomotor mode, (c) by substrate use [Color figure can be viewed at wileyonlinelibrary.com]

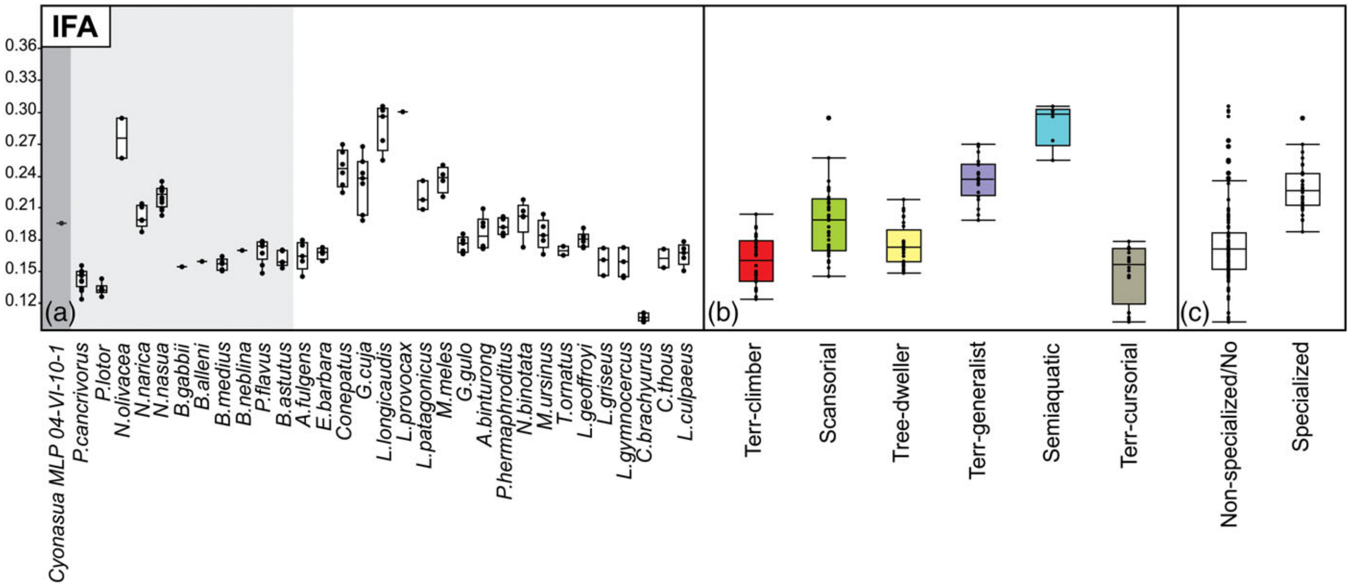

FIGURE 16 Boxplot of index of Fossorial ability (IFA). For explanation, see Figure 13. (a) by taxon, (b) by substrate preferences and locomotor mode, (c) by substrate use [Color figure can be viewed at wileyonlinelibrary.com]

The degree of medial orientation of the *processus coracoideus* in *Cyonasua*, also observed in the scansorial and digger *N. nasua*, would lengthen the lever arm of the *m. coracobrachialis*. This helps to keep the humerus in position and give it some advantage for maintaining contact with arboreal substrates, as observed in other mammals (Davis, 1964; Ercoli, Álvarez, Stefanini, Busker, & Morales, 2015; Sargis, 2002; Taylor, 1974). Possibly, in *Cyonasua* this muscle contributed to the gleno-humeral joint stabilization against mechanical demands (e.g., digging, food manipulation).

4.2 | Functional morphology of humeral features

Greater bone robustness has been linked to the requirements of body support (see regression results) during locomotion, or to the development of forces required for specific functions of the limb such as digging or food manipulation (Elissamburu & De Santis, 2011; Samuels et al., 2013; Samuels & Van Valkenburgh, 2008; Toledo et al., 2012). Thus, the robust humerus of *Cyonasua* (relatively high HRI value) is related to the ability to resist relatively high bending and shearing stresses, which would be associated with supporting their body mass (body mass average for *Cyonasua*: 19.5 kg., greater than any extant procyonid; Tarquini et al., 2018), as could be suggested by the low but significant positive allometry of HRI. However, given that the HRI values of *Cyonasua* were close to those of *Nasua*, *Nasuella*, and *Conepatus*, genera in which body masses are small to moderate (4.5 kg on average for *Nasua*, Gompper, 1995; Gompper & Decker, 1998; 1.34 kg for *Nasuella*, Jones et al., 2009; 2 kg on average for *Conepatus*, Kasper et al., 2012), but all of which are specialized diggers among carnivorans, it is likely that this robustness is related to stresses caused by active use of the forearm in digging, rather than supporting body mass. In this sense, *Cyonasua* shows values of HRI that coincide with the median for the SU-specialized-digger category.

4.3 | Functional morphology of the elbow joint

The elbow joint complex comprises the distal humeral epiphysis, the proximal ulnar and radial epiphyses and the lever arm formed by humerus and ulna. This joint transfers loads between the upper and lower arm segments and provides stability while at the same time allows for mobility (Evans & de Lahunta, 2013; Jenkins Jr., 1973). Such movements involve not only flexion-extension, but also pronation–supination, in which the radius rotates medio-laterally around the ulna, allowing in some cases the palm of the hand to be oriented medially (semisupination), and even dorsally (supination; Andersson, 2004b; Fabre et al., 2013). These types of movements (pronation-supination) occur to diverse degrees in all extant procyonids (McClearn, 1992; Wilson & Mittermeier, 2009).

The shape of the humeral condyle is slightly variable among the *Cyonasua* specimens examined. Generally speaking, the condyle of *Cyonasua* is deeper compared to those of extant SA procyonids. The trochlea of *Cyonasua* suggests a stabilized elbow joint for flexion-extension, with some restriction of lateral movements of the radius, and substantial transfer of forces with restriction of movements outside the parasagittal plane; similarly to the condition in other mammals (Andersson, 2004a; Candela & Picasso, 2008; Jenkins Jr., 1973; Sargis, 2002; Taylor, 1974). The trochlear articular surface, smaller than the surface of the *capitulum* and the lateral margin of the humeral condyle, indicates that *Cyonasua* would have had some degree of pronation-supination movements, as observed in other carnivorans (Taylor, 1974) and rodents (Candela & Picasso, 2008). These morpho-functional inferences were partly coincident with HCDI values. The relatively lower HCDI for all fossil specimens analyzed compared to extant procyonids and most carnivorans analyzed (except canids, with lowest HCDI values), is consistent with a stabilized morphology. The HCDI values for *Cyonasua* were similar to those of the terrestrial-climber *Procyon* and the scansorial and digger *Nasuella*, among procyonids. In addition, the HCDI values of *Cyonasua* were similar to those of *Meles meles*, a generalized mustelid with marked digging abilities, and close to *Leopardus* *geoffroyi*, a terrestrial-climber. HCDI values were highest for all tree-dwelling taxa (*Bassaricyon*, *Potos*, *Arctictis*, and *Nandinia*), in which a more latero-medially extended surface and poorly developed trochlea provide a wide and shallow surface for ulnar and radial movements and, in consequence, allow pronation-supination movements that are advantageous for arboreal carnivorans. Such movements are minimal in cursorial species (Salesa, Anton, Peigné, & Morales, 2008; Taylor, 1974), and consequently, HCDI values are lowest in terrestrial-cursorial forms, in which a deep condyle produces a hinge-like joint, with movement occurring predominantly in the parasagittal plane.

The olecranon fossa is functionally important for forearm extension and elbow joint stability, and its depth has been linked to greater extension of the zeugopodium during terrestrial locomotion (Argot, 2001; Flores & Díaz, 2009; Sargis, 2002; Szalay & Dagosto, 1980; Taylor, 1974). According to the latter, the morphology of the olecranon fossa in *Cyonasua* would have allowed a wide range of forearm extension, although probably not as wide as in *P. cancrivorus*, the most specialized for terrestrial habits among extant procyonids. However, in other living procyonids, the olecranon fossa is shallower and they may even present an anteriorly directed *olecranon*, which may reflect partial extension of the ulna. This condition would be associated with limited stability during forelimb extension, a somewhat mobile elbow joint and frequently flexed posture, and characteristics than in other mammals are associated with arboreal habits (Argot, 2001; Candela & Picasso, 2008; Taylor, 1974).

The entepicondyle provides an area for attachment of most autopodial flexor muscles, and its enlargement increases the areas of origin for the manual and digital flexors and the forearm flexor *pronator teres* muscle (Davis, 1964). The development of the entepicondyle improves mechanical advantage for increased strength during flexion of digits, flexing the wrist and stabilizing the shoulder (Hildebrand, 1985). The entepicondyle of *Cyonasua* indicates good development of the flexor and pronator muscles, probably greater than that of *P. cancrivorus*, but not as much as in *N. nasua* and *N. olivacea*, in which it results in improved mechanical advantage for the digging muscles (Gompper & Decker, 1998; Hildebrand, 1985; McClearn, 1992; Samuels et al., 2013). According to Argot (2001), a medial extension of the entepicondyle allows inferring some grasping ability of the autopodium. However, Fabre, Cornette, Slater, et al. (2013) suggest radial features associated with this ability and propose that the shape of the humerus and ulna seem to be more influenced by force transfer. The use of the forelimb to grasp objects (e.g., food) is common among Carnivora, especially in tree-dwelling taxa (Fabre, Cornette, Slater, et al., 2013). Nevertheless, these entepicondylar features would not be directly associated with grasping ability, as Tarquini et al. (2017) showed that *Cyonasua* sp. (MLP 04-VI-10-1) had poor grasping ability and that entepicondylar development was not an influential variable in their analyses of this capability.

Additionally, the orientation of the entepicondyle relative to the trochlea is another feature to analyze in the elbow joint. According to Jenkins Jr. (1973), a caudal orientation and shortening of the entepicondyle decrease the torque exerted by flexor muscles at the elbow joint, as the flexors pass behind rather than medially to the trochlea (Jenkins Jr., 1973). These traits have their maximum expression in cursorial mammals (Wang, 1993). Thus, the slightly caudal orientation of the entepicondyle, in association with the deep *olecranon* fossa and deep humeral trochlea of *Cyonasua*, would reflect restricted movements within the sagittal plane, suggesting a tendency to terrestrial habits similar to that of *Procyon*. Furthermore, Ginsburg (1961) associated a well-developed and posteriorly directed entepicondyle with plantigrade forms in ursids. According to this, the features of *Cyonasua* would suggest plantigrady.

The shape of the ulnar trochlear notch and its correlation with function and diverse ecological habits have been analyzed in other mammalian taxa (Argot, 2001, 2003; Taylor, 1974). The trochlear notch of *Cyonasua* indicates a wide range of forelimb extension at this level, as well as a relatively deep olecranon fossa. However, some of the abovementioned features, such as an extended humeral trochlea, slight proximal extension of the lateral margin of the articular condyle and the caudal inclination of the entepicondyle, are consistent with a stabilized elbow joint. Among extant SA procyonids, *Potos flavus*, *Bassaricyon*, and *Nasua nasua*, with tree-dwelling and scansorial habits, present a wide trochlear notch.

The asymmetric *processus anconeus* would allow increased contact with the lateral and caudal humeral condyle surfaces, and prevent the ulna from pulling away medially in supination movements, as in other mammals (Argot, 2003; Taylor, 1974). Thus, the asymmetric *processus anconeus* of *Cyonasua* would have contributed to stabilization of the elbow joint when the zeugopodium was extended.

The *olecranon* represents the in-lever arm of *m. triceps brachii*, involved in extension of the zeugopodium (Evans & de Lahunta, 2013), as well as in stabilizing the elbow joint when standing (Fisher, Adrian, Barton, Holmgren, & Tang, 2009). The shape and length of the *olecranon* of *Cyonasua* are shared with both terrestrial-cursorial and other categories associated with climbing habits (tree-dwellers, scansorials, and terrestrial-climbers). In contrast, diggers (e.g., *Nasua*, *Nasuella*, *Meles*, *Conepatus*) present a prominent, proximally extended *olecranon*, associated with an increase of the action of *m. triceps brachii* during forearm and hand extension. This provides greater in-lever arm that favors force over speed (Elissamburu & Vizcaíno, 2004; Maynard-Smith & Savage, 1956; Van Valkenburgh, 1987; Vizcaíno, Milne, & Bargo, 2003). In particular, the *olecranon* is straight or deflected caudally in terrestrial species, increasing the lever arm when the elbow joint is extended, while in most climbers the *olecranon* is curved cranially, maximizing the lever arm of *m. triceps brachii* when the elbow joint is flexed (Van Valkenburgh, 1987). In *Cyonasua*, the *olecranon* is straight as in the terrestrial-climbing procyonid *P. cancrivorus* and other carnivorans with similar habits (e.g., *Gulo gulo*, *Leopardus geoffroyi*) or more specialized climbers (e.g., *Eira barbara*). Thus, the forces produced by *m. triceps brachii* are maximized when the angle between stylopodium and zeugopodium is about 90° (semiflexion). In quantitative terms, *Cyonasua* had relatively high values for IFA, similar to *Nasua*; which can be associated to a powerful lever arm. This combination of traits in *Cyonasua* would point out to a semi-flexed elbow joint, not reaching the more crouched limb stance of arboreal procyonids (e.g., *Potos*, *Bassaricyon*), but probably more crouched than *Procyon* (in which the *m. triceps brachii* helps to support the body in the propulsive phase of terrestrial locomotion, as in other mammals, for example, Taylor, 1974; McClearn, 1992; Argot, 2001). In addition, the *m. triceps brachii* would have exerted greater force in *Cyonasua* compared to that of *Procyon*, but not as much as in *Nasua*.

Additionally, the *olecranon* is related to attachment of *m. anconeus*, an in-lever arm extensor of the forearm that acts as an initiator and elbow joint stabilizer (Evans & de Lahunta, 2013; Fisher et al., 2009). According to Argot (2001), this muscle acts in flexed stances, when the elbow is abducted, and the distal parts of the forelimb are pressed against the medially lying arboreal substrate. The development of the lateral supracondylar crest in most specimens of *Cyonasua* indicates that this muscle would contribute considerably to both extension and stabilization of the elbow joint, probably more than in *P. cancrivorus*. Furthermore, the considerable proximo-distal extension of the lateral supracondylar crest in most specimens of *Cyonasua* would increase the lever arm of *m. brachioradialis* for elbow joint flexion, as in other mammals (Argot, 2001). Interestingly, the *m. brachioradialis* (formerly called the *supinator longus*) is directly associated with climbing because it is most active when the hand is in the prone or semiprone position, during quick flexion or flexion against resistance (Argot, 2001; Pauly, Rushing, & Scheving, 1967). Thus, this lateral crest is well developed in climbers, as seen in most extant SA procyonids and *Cyonasua*. In cursorial mammals such as canids, however, the lateral supracondylar crest is considerably narrower and the *m. brachioradialis* is reduced or absent (Evans & de Lahunta, 2013; Fisher et al., 2009); in this sense, canids have lost some of the ability to supinate their manus (De Souza Jr., dos Santos, Nogueira, Abidu-Figueiredo, & Santos, 2015).

4.4 | Functional morphology of ulnar and radial features

The straight to slightly convex caudal margin (in latero-medial view) of the ulnar diaphysis in *Cyonasua* has also been observed in the terrestrial-climber *P. cancrivorus*, as well as in other terrestrial (Argot & Babot, 2011; Taylor, 1974) and arboreal taxa (Fabre, Cornette, Slater, et al., 2013). In the latter, this character is thought to facilitate the transmission of compressive loading and likely relates to the importance of this bone in load transfer and stability of the forelimb (Fabre, Cornette, Slater, et al., 2013). However, in contrast with the condition of *P. cancrivorus*, the ulnar diaphysis of *Cyonasua* is shorter and more robust, which could be associated with resistance to diverse stresses (e.g., body mass) at the expense of reducing locomotion efficiency, as in other carnivores (Martín-Serra, Figueirido, & Palmqvist, 2014, 2016).

The slightly medial concavity of the ulnar diaphysis in *Cyonasua* would reflect the good development of flexor muscles of the autopodium (e.g., *m. flexor digitorum profundus*, *m. flexor carpi ulnaris*). The actions of these muscles are important in both digging, as in *N. nasua* and *N. olivacea*, and food manipulation. The development and location of the medial distal crest of the ulnar diaphysis, site of attachment of *m. pronator quadratus*, is related with autopodium movements (Argot, 2003; Taylor, 1974; Toledo et al., 2013). This muscle is involved in the maintenance of structural integrity between radius and ulna near the carpus, as the forces imposed on this mobile part of the forearm would tend to dislocate it (Argot, 2003). Thus, the characteristics found in *Cyonasua* would be associated with a strong relationship between ulna and radius that would allow withstandings mechanical stresses, but with some degree of advantage for pronation-supination of the autopodium.

The robust styloid process of the ulna in *Cyonasua* indicates relatively high mechanical demands between this bone and the ulnar carpal. The distal articular facet for articulation with the radius is related to rotation of the latter from pronate to semisupinate or supinate position. The cranial extension of the distal articular facet observed in *Cyonasua* could allow it some degree of rotation of the radius with respect to the ulna, resulting in a semisupinated autopodium; as observed in other carnivores (Taylor, 1974).

The radial head articulates with both the *capitulum* and the radial notch, and these are linked with pronation-supination movements, force transmission and stability (Argot, 2001; Fabre, Cornette, Slater, et al., 2013). The shape of the radial notch and radial head in *Cyonasua* resemble those of *P. cancrivorus*, which present a wide supination range (e.g., semisupination) and intermediate grasping ability (Fabre, Cornette, Slater, et al., 2013; Tarquini et al., 2017). However, in contrast with *P. cancrivorus*, in *Cyonasua* the lateral margin of the radial head is extended, which would have provided greater elbow stability during flexion, as suggested in other mammals (Argot, 2001; Szalay & Dagosto, 1980). In this aspect, *Cyonasua* resembles *N. nasua*, which presents a certain degree of elbow immobility in association with the requirements for digging.

The distal carpal surface and the *processus styloideus* of the radius have been previously analyzed in other mammals (Argot, 2001; Martín-Serra et al., 2014). The features found in the distal carpal surface of *Cyonasua* (e.g., pyriform shape, latero-medially extension) are associated with good flexion-extension movements of the wrist; however, the range of abduction-adduction would be somewhat restricted. The development of the *processus styloideus* observed in *Cyonasua* would provide stability to the wrist joint, while the distal surface perpendicular with respect to the radial diaphysis could be linked to poor grasping ability in *Cyonasua*, in agreement with a previous quantitative analysis (Tarquini et al., 2017) and similarly to other carnivores (Fabre, Cornette, Slater, et al., 2013; Fabre, Marigó, Granatosky, & Schmitt, 2017).

4.5 | Functional morphology of autopodial features

Although only few autopodial elements have been preserved, they indicate that the autopodium of *Cyonasua* had a short robust manus compared to other forelimb elements and to extant SA procyonids. This would be associated with relatively high mechanical demands on the autopodium, as observed in digging mammals (Hildebrand, 1985; Lessertisseur & Saban, 1967; Moore, Budny, Russell, & Butcher, 2013; Morgan & Verzi, 2011; Polly, 2007), that present well developed flexor muscles of the carpus (*m. flexor carpi ulnaris*) and digits (*m. flexor digitorum profundus*).

The shortened metacarpals of *Cyonasua* could be related to a plantigrade stance and poor grasping ability, as observed in other mammals (Argot, 2003; Ginsburg, 1961) and in agreement with a quantitative analysis of *Cyonasua* (Tarquini et al., 2017). Furthermore, the extension of the proximal facet of metacarpal I in *Cyonasua* would indicate a wide flexion-extension range for this digit.

FIGURE 17 Artistic reconstruction of *Cyonasua* by Martina Charnelli

4.6 | Summary of functional morphology inferences

Comparisons with extant SA procyonids indicate that *Cyonasua* (Figure 17) mostly resembles *Nasua nasua* and *Procyon cancrivorus*, even though extinct procyonids presented particular features. This is in agreement with phylogenetic hypotheses based on morphological characters (i.e., craniodental characters) that consider these taxa as close relatives (Ahrens, 2012; Baskin, 2004; Decker & Wozencraft, 1991), in contrast to molecular hypotheses (Fulton & Strobeck, 2007; Koepfli et al., 2007).

According to the previous results, the morphology of the pectoral girdle and forelimb of *Cyonasua* indicates strongly stabilized joints, powerful mechanical advantage for humeral protrusion and abduction, and for elbow extension. Some features indicate restriction of movements to the parasagittal plane, while others are associated to a certain freedom in the range of movements. The forelimb would have had moderate supination ability (semi-supination), with poor grasping ability, and a slightly more flexed posture than *Procyon*. Furthermore, the robust forelimb elements of *Cyonasua* reflect considerable transfer of loads between the different forelimb elements, possibly related to their relatively large body mass (mean body mass 19 kg for *Cyonasua*; Tarquini et al., 2018) but also advantageous for resisting stresses occasioned by forelimb activities (digging, prey capture, etc.). Thus, our present findings provide additional support to a previous quantitative approach (Tarquini et al., 2017, 2018), in which *Cyonasua* was characterized as a generalized terrestrial form with climbing abilities and poor grasping ability, but without excluding some digging ability. It is worth noting that the poor grasping ability inferred for *Cyonasua* would not imply inability to climb, given that extant procyonids include climbing forms with similar grasping-ability values (e.g., *Nasua*; Fabre, Cornette, Slater, et al., 2013).

4.7 | Paleoecological remarks

Body mass is one of the most interesting ecological variables to be considered in paleobiological studies due to its great influence on both ecological and physiological factors (Gittleman, 1985; Hildebrand, 1988; Johnson, 2002; McNab, 1973; Peters & Raelson, 1984; Peters & Wassenberg, 1983; Schmidt-Nielsen, 1984; Tarquini et al., 2018; Van Valkenburgh, Wang, & Damuth, 2004; Vizcaíno, Bargo, Cassini, & Toledo, 2016;). Thus, considering its substrate preference and locomotor mode, and its relatively large body mass, *Cyonasua* would has been limited climbing ability, and hence was probably constrained to moving on strong supports, probably climbing to rest, forage or avoid predators, as suggested by Tarquini et al. (2018). Furthermore, *Cyonasua* showed similarities in some indexes (HDEWI and IFA) with medium-sized to large forms that possess good or moderate climbing abilities, such as the binturong (*Arctictis binturong* ~ 13 kg, Jones et al., 2009) and the sloth bear (*Melursus ursinus* ~ 104 kg, Jones et al., 2009 Wilson & Mittermeier, 2009).

Regarding dietary adaptations, the strong, stabilized and relatively short pectoral girdle and forelimbs, would be well suited for digging or prey manipulation. This is in agreement with the omnivorous diet inferred for *Cyonasua*, although it would have been more carnivorous and occupying a more predatory niche than extant procyonids (Ameghino, 1885; Prevosti & Forasiepi, 2018; Soibelzon, 2011; Tarquini et al., 2018). According to Woodward et al. (2005), predators are usually between one and three orders of magnitude larger than their prey in terms of body mass. However, Carbone, Teacher, and Rowcliffe (2007) consider that larger species (>15–20 kg), in the range of mass inferred for *Cyonasua* (Tarquini et al., 2018), prefer prey around their own size. Therefore, the dental morphology, larger size, and strong forelimbs of *Cyonasua* suggest it possibly had access to relatively larger prey than those available for extant procyonids. In agreement with this, Cenizo, Soibelzon, and Magnussen Saffer (2016) reported predatory action of *Cyonasua* on *Thylophorops chapadmalensis*, a didelphid with a body mass of about 6 kg. (Goin, Zimicz, de los Reyes, & Soibelzon, 2009).

During the time when *Cyonasua* was recorded (late Miocene to late Pliocene), South America presented diverse climatic conditions, characterized by increasing aridity and cold that culminated in three major glacial events around 2.5 MYBP (Denton, 1999; Le Roux, 2012a, 2012b; McKay et al., 2012; Zachos, Pagani, Sloan, Thomas, & Billups, 2001). Open environments were in expansion, and savannahs, plains, xerophytic woods and gallery forest alongside water bodies were predominant. Environmental studies of the sedimentary units bearing *Cyonasua* remains agree with these global events (e.g., studies on Fm. Andalhuala, Bonini, Georgieff, & Candela, 2017; Bossi & Muruaga, 2009; Fm. Chapadmalal, Erra, Osterrieth, Morel, & Fernández-Honaine, 2010). The mammalian assemblages recorded before the arrival of procyonids (early Miocene) comprised several herbivorous lineages (endemic ungulates, xenarthrans, argyrolagid and paucituberculatan marsupials, primates, and caviomorph rodents) and endemic marsupials assemblages with omnivorous, mesocarnivorous and hypercarnivorous forms, including sparassodonts as top predators with ample diversity of body size and habits (Bargo & Vizcaíno, 2008; Benedetto, 2010; Cifelli, 1985; Croft, 1999, 2006; Goin, Montalvo, & Visconti, 2000; MacFadden, 2005; Ortiz-Jaureguizar & Cladera, 2006; Patterson & Pascual, 1968; Prevosti, Forasiepi, & Zimicz, 2013; Reig, 1981; Scillato-Yané, 1986). In addition, a characteristic and diverse avian lineage, the predatory phorusrhacoids or "terror birds" (Phorusrhacidae; Ameghino, 1895; Tambussi, 2011; Tambussi & Noriega, 1996) was also recorded alongside these mammals. Given the wide diversity of South American avian and mammalian predators that were coeval and potentially shared trophic and spatial resources with *Cyonasua*, its forelimb functional capabilities, diet, and body mass would have allowed it to prey on small and medium vertebrates, as well as to avoid some of these dominant predators. The combination of these features and abilities would have allowed the success of this genus in South America for a long period, which spanned from the late Miocene to the early Pleistocene.

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AUTHOR CONTRIBUTIONS

Tarquini J. conducted the research, compiled the raw data for analyses, wrote complete drafts of the manuscript and made the figures. Morgan C. C. and Toledo N. participated in the morpho-functional and statistical analyses and edited later drafts of the manuscript. Morgan C. C., Toledo N. and Soibelzon L. H. were involved in the edition of a later draft of the manuscript, revision and final approval of the manuscript.

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