RESEARCH ARTICLE

Is the Shape of Turtle Claws Driven by Locomotor Modes?

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Abstract

Claws are the most common attachment mechanism in vertebrates. The comparative anatomy and morphology of claws has been studied mainly in reptiles and birds. However, as far as we know, studies focusing on turtles' claws are lacking. Turtles occupy a wide range of habitats, from aquatic to terrestrial, and vary in form and behavior, being an ideal model organism for ecomorphological studies. We performed qualitative and quantitative analyses to find a relationship between morphological variation and both ecological factors and phylogenetic constraints that could have driven the evolution of turtles' claws. The claws of 35 adult turtle and tortoise specimens of 12 species of testudines with different locomotor modes were compared. Our data show several convergence traits in claw shape, with convergence being reinforced by the low phylogenetic signal exhibited by most characters. We propose that claw morphology in turtles is mainly associated with some mechanical functions, such as freshwater-swimming, bottom-walking and tearing of prey.

Keywords Claws · Ecology · Morphology · Testudinidae

Introduction

Ecomorphology investigates whether species that inhabit a wide range of environments and/or exhibit diverse locomotor modes display differential morphologies that can be related to different ecological factors (Williams, 1972; James, 1982; Arnold, 1983; Losos, 1990, 2009). In fact, the capability of those species to perform a particular task relevant to their ecology may elicit differences in morphology (Butterfield et al., 2020). In the last decades, qualitative and quantitative analyses of the relationships between morphological variation and both ecological factors and phylogenetic constraints have increased considerably (Angielczyk et al., 2015; Björklund & Merilä, 1993; Claude et al., 2004; Klingenberg & Ekau, 1996; Lande & Arnold, 1983; Tulli et al., 2009, 2016; Wyneken & Salmon, 2020; Zani, 2000). Most of them have focused on proportions of fore and hind limbs (Herrel et al., 2001; Kohlsdorf et al., 2001; Fabre et al., 2015; Blob et al., 2016), skull shape (Herrel et al., 2007; Watanabe et al., 2019), shell shape (Benson et al., 2011), and claws (D' Amore et al., 2018; Hahn et al., 2014; Tulli et al., 2009, 2016; Zani, 2000).

Claws are epidermal-derived and strongly keratinized structures that wrap around the tapering terminal phalanges of each digit (Hildebrand, 1995). Claws are the most common grip mechanism in vertebrates (Zani, 2000). The comparative anatomy and morphology of claws have been studied in detail mainly in reptiles (Zani, 2000; Tulli et al., 2009; D' Amore et al., 2019; Alibardi, 2020; Mann et al., 2021) and birds (Feduccia, 1993; Hahn et al., 2014). As far as we know, studies focusing on turtles' claws are lacking.

In reptiles, such as lizards, sharply curved claws allow them to adhere to rough substrates and climb on rocky boulders or trees, whereas long and shallow claws allow them to dig the sandy substrate to bury or dive into it (Tulli et al., 2009, 2011; Zani, 2000). Turtles use claws to help them to clamber onto riverbanks and floating logs

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on which they bask, and to climb cliffs for nesting (López et al., 2013). Male turtles tend to have particularly long claws that seem to be used to stimulate the female while mating (Wyneken, 2001). While most turtles have webbed feet, some, such as the pig-nosed turtle (*Carettochelys insculpta*), have true flippers, with the digits fused into paddles and with relatively small claws (Beggs et al., 2011).

Turtles occupy a wide range of habitats, from aquatic to terrestrial, and vary in forms and behaviors, being an ideal model organism for ecomorphological studies. Niche divergence, including dietary and habitat shift, could be correlated mainly with head size, limbs, shell shape and tail traits (Claude et al., 2003; Jaffe et al., 2011; Rivera, 2008; Rivera et al., 2014). To our knowledge, there is no previous study comparing claw configurations in turtles to correlate them with ecological factors and phylogeny. In this work, we performed qualitative and quantitative analyses to explore possible links between morphological variation and both ecological factors and phylogenetic constraints that could have driven the evolution of turtles' claws. Based on the hypothesis that the claws are active devices to improve locomotion, we predict that the freshwater turtles will show the longest claws allowing the increase of powerful forelimb extension required to push through the dense fluid medium. In contrast, terrestrial forms will present the shortest and curved claws, which could provide better support on dry and hard substrates. This work allows us to complement a broader study on the ecomorphology and evolution of the claws of tetrapods, focusing on the effect of ecological factors that could have molded the shape of the tetrapod claws (Tulli et al., 2009, 2016).

Materials and Methods

Data Collection

We examined 35 adult turtle and tortoise specimens of 12 species of testudines: *Acanthochelys pallidipectoris* (6), *Chelonoidis chilensis* (3), *Hydromedusa tectifera* (4), *Kinosternon scorpioides* (3), *Mesoclemmys vanderhee* (3), *Phrynops hilarii* (8), *Phrynops geoffroanus* (1), *Podocnemis unifilis* (1), *Trachemys dorbigni* (2), *Trachemys scripta* (4), *Terrapene carolina* (1), and *Testudo graeca* (1). Specimens were selected to represent several locomotor modes, including specialized taxa belonging to independent evolutionary lineages. All the examined specimens are housed in systematic collections and listed in the supporting information (Supplementary material 1). Since the materials analyzed are all housed in collections, no ethical issue was raised.

Morphology

For qualitative and quantitative analyses, a set of characters hypothesized to be related to the different locomotor modes was chosen based on previous studies (Tulli et al., 2009, 2016; Zani, 2000). The claws of all digits and toes from the right the limbs were photographed in lateral view under a binocular microscope (Leica ID M-Series) (Fig. 1). Then an outline of the claw types of each locomotor mode (Table 1) was drawn for illustrative purposes using Inkscape
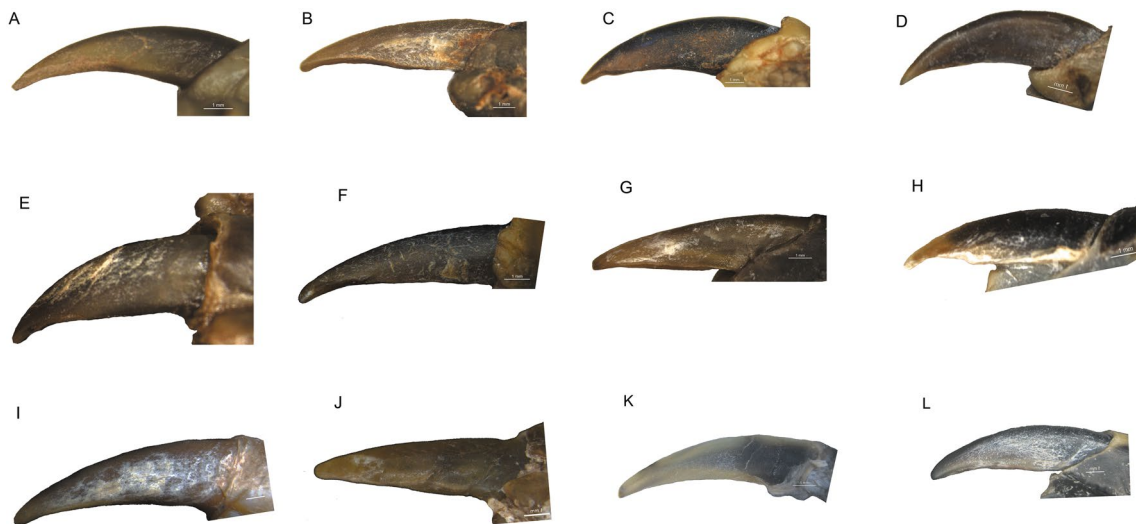

Fig. 1 Captured images of lateral view of claw morphology of 12 species of Testudinidae. **A.** *Acanthochelys pallidipectoris,* **B.** *Chelonoidis chilensis,* **C.** *Hydromedusa tectifera,* **D.** *Kinosternon scor-pioides,* **E.** *Mesoclemmys vanderhee,* **F.** *Phrynops geoffroanus,* **G.** *Phrynops hilarii,* **H.** *Podocnemis unifilis,* **I.** *Terrapene carolina,* **J.** *Testudo graeca,* **K.** *Trachemys scripta,* **L.** *Trachemys dorbignyi*

Table 1 - Locomotor modes of the examined species, based on data from the literature, and claw shapes illustrating qualitative differences among species belonging to different ecological groups

| Species	Authors	Claw shape	Locomotor modes
Acanthochelys pallidipectoris	Richard (2000)		
Mesoclemmys vandderhee	Cassano (2017)		Freshwater-swimmer
Phrynops hilarii	Lopez et al. (2013)		
Phrynops geoffranus	Richard (2000)		
Podocnemis unifilis	Norris et al. (2011)		
Chelonoidis chilensis	Richard (2000)		
Terrapene carolina	Kiester and Willey (2015)		Terrestrial-walker
Testudo graeca	Andreu et al. (2004)		
Trachemys dorbigni	Munteanu (2014)		
Trachemys scripta	Munteanu (2014)		Bottom-walker
Hydromedusa tectifera	Alcalde et al. (2021)		
Kinosternon scorpioides	Berry & Shine (1980), Munteanu (2014)		
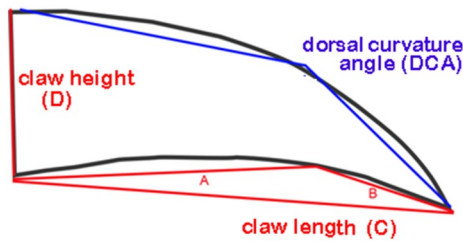
Fig. 2 Morphological measurements used in this study modified from Zani (2000). A = distance from the claw base to the point of inflexion of the claw; B = distance from the point of the inflexion of the claw to the tip of the claw; C = claw length; D = claw height; DCA = dorsal curvature angle

1.0.2 (Vieites Fariña, 2003–2020). The captured images were measured and analyzed under a Leica M205 stereomicroscope using the software LAS V4.8.Ink. We performed a quantitative analysis to assess the degree of claws' morphological specialization and different locomotor modes (Table 1). The number of adult specimens per species varied according to availability (range 1–7). Body size (BS) was measured as carapace curve length (CCL), from the anterior edge of the nuchal scales to the posterior edge of the caudal scale, in the animals stored in 70% alcohol. Measurements of the specimens were taken using a measuring tape. Claws were measured following Zani (2000) and included height, length, and ventral and dorsal curvature (Fig. 2). Measurements of the claws of limbs and body size are reported as supporting information (Supplemental Table 1).

Locomotor Modes

The species were classified considering three categories of locomotor modes: bottom-walker, freshwater-swimmer, and terrestrial-walker (Table 1). Bottom-walkers are specimens that walk on the bottom of rivers, lakes and other types of slow-moving water courses, and rarely swim (Berry & Shine, 1980; Willey & Blob, 2004; Munteanu, 2014). Freshwater-swimmers are turtles that inhabit freshwater environments and spend their lives mostly in the water; they can also look for places to sunbathe and clamber onto riverbanks and floating logs where they bask or even nest (López et al., 2013) (Table 1). Terrestrial-walkers are turtles that spend their lives in terrestrial habitats with scarce or no occurrence in wet environments; they walk long distances looking for food, nests or refuges (Mao et al., 2015). We realize that the average turtle is capable of exhibiting a broad range of locomotor modes; therefore, we categorized the different locomotor modes based on the one most frequently used by the taxa (Table 1).

Phylogeny

Phylogenetic Comparative Analyses were performed using a composite tree (Fig. 3) based on Guillon et al. (2012), Ferreira et al. (2018), and Evers and Benson (2019); the latter two were used to fill the gaps of species not considered in Guillon et al. (2012). Because our reconstructed phylogeny did not have defined branch lengths, the tree was fitted to ultrametric using 'nnls.tree', a function of
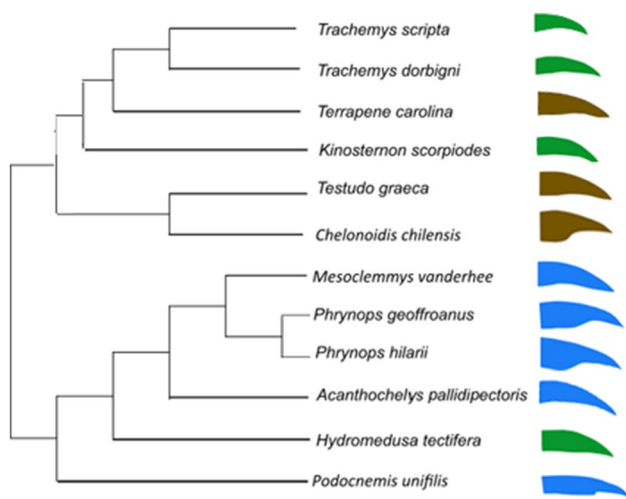
Fig. 3 Composite cladogram of Testudinidae evaluated in our study based on the results of several morphological and molecular studies (Guillon et al., 2012; Ferreira et al., 2018; Evers and Benson, 2019). The individual groups with their own claw shape in relation to locomotory modes are shown

'phargon' package (Schliep et al., 2011). This function estimates the branch length using non-negative least squares given a tree and a distance matrix forcing it to ultrametricity (Schliep et al., 2011).

Statistical Analysis

Mean values of claw traits per species were $\log_{10}$ transformed prior to analyses to fulfill normality assumptions. Since locomotor modes are expressed in proportions, ecological data were arcsine square root transformed (Martin & Bateson, 1999). All statistical analyses were implemented in an R statistical environment (R version 4.2.1; R Development Core Team, 2022).

Morphological traits require body size corrections based on their phylogenetic context; therefore, we performed the phylogenetic size correction analysis described by Revell (2009). Residuals were calculated from least square regression analyses of morphological traits on body size (BS), and phylogenetic non-independence was controlled using phylo.resid (a module of Phytools for R developed by Revell, 2012). The resulting residuals were then used for the subsequent analyses. To reduce the number of variables and at the same time to identify correlated evolution among traits we run a phylogenetically-based Principal Component Analysis (PCA) based on a variance–covariance matrix of the morphological residuals using a Varimax rotation, implemented with the module Phyl.PCA from the Phytools package for R (Revell, 2012). From these analyses, we obtained the species scores and morphological loadings corresponding to the first three principal components in relation to approximately 70%

Table 2 Scores resulting from the principal component analysis (PC1, PC2 and PC3) performed with morphological variables. Abbreviates: D: correspond to digits, d: toes, CC: claw curvature, CH: claw height, CL: claw length, DCD: curvature dorsal

Variables	PC1	PC2	PC3
CCDI	0.07	0.51	**0.68**
CHDI	**−0.89**	−0.39	−0.16
CLDI	**−0.89**	−0.42	0.16
CCDII	−0.58	−0.21	0.27
CHDII	**−0.89**	−0.34	−0.14
CLDII	**−0.93**	−0.27	0.21
CCDIII	−0.51	0.35	−0.41
CHDIII	**−0.94**	0.09	−0.03
CLDIII	**−0.95**	0.13	−0.01
DCDIV	0.17	0.13	0.11
CCDIV	0.12	0.18	**0.65**
CHDIV	**−0.94**	0.15	−0.10
CLDIV	**−0.83**	0.06	−0.48
DCDV	−0.20	**−0.69**	−0.33
CCDV	−0.30	0.03	**−0.75**
CHDV	**−0.95**	0.26	0.12
CLDV	**−0.94**	0.22	0.17
CCT1	0.00	0.28	−0.64
CHT1	**−0.96**	−0.08	−0.09
CLT1	**−0.94**	−0.07	0.09
CCT2	0.05	**0.65**	−0.60
CHT2	**−0.99**	0.02	0.00
CLT2	**−0.92**	−0.19	0.06
DCT3	0.01	0.32	−0.18
CCT3	0.49	0.17	**0.60**
CHT3	**−0.98**	0.04	−0.08
CLT3	**−0.99**	−0.04	0.07
DCT4	0.25	**0.65**	−0.16
CCT4	0.24	0.23	**−0.61**
CHT4	**−0.95**	0.25	−0.03
CLT4	**−0.94**	0.17	0.14

of accumulated variance. To detect the variables from the morphological loadings, with the greatest contributions to each Principal Component (PC), we considered informative only those vectors with higher absolute values (negative or positive; Table 2 in boldface). Three principal components were retained by carefully examining a scree plot and the eigenvectors of each principal component via the broken stick rule (Jackson, 1993) (Table 3). Statistical significance of the PC was evaluated following the Broken-stick test (Peres-Neto et al., 2005). Then, using those informative traits, we tested for differences among them and these values were used as input for the following analyses.

Subsequently, we tested three different evolutionary models to explore the processes that best explain the evolution of these morphological traits. The first model, known as

Table 3 Values of AICc and Log Likelihood (LogL) corresponding to the evolutionary models tested (Brownian motion [BM], Ornstein–Uhlenbeck [OU] and Early Burst [EB]) of morphological variables. wAICc is the weight of the different models in boldface. BeMo indicates the evolutionary model that best fitted the data based on the wAICc values

Variables	K	p-value	Lambda	p-value	BM	OU	EB	BeMo
CCDI	0.5	0.481	0.0001	1.000	0.317	**0.631**	0.05	OU
CHDI	0.608	0.224	0.990	0.449	0.405	**0.495**	0.099	OU
CLDI	0.577	0.283	0.093	0.871	**0.442**	**0.452**	0.106	BM-OU
CCDII	**0.926**	**0.04**	0.99	0.06	0.068	0.042	**0.888**	EB
CHDII	0.706	0.11	0.99	0.16	**0.581**	0.297	0.122	BM
CLDII	0.552	0.33	0.0001	1	0.401	**0.486**	0.112	OU
CCDIII	0.450	0.64	0.0001	1	0.210	**0.750**	0.035	OU
CHDIII	**0.946**	**0.01**	0.99	0.03	**0.472**	0.116	0.411	BM
CLDIII	0.665	0.165	0.99	0.5	**0.577**	0.32	0.101	BM
CCDIV	0.452	0.67	0.00007	1	0.357	**0.5855**	0.0571	OU
CHDIV	0.733	0.108	0.788	0.365	**0.683**	0.207	0.109	BM
CLDIV	0.4	0.83	0.00007	1	0.137	**0.84**	0.022	OU
CCDV	0.356	0.970	0.0001	1	0.124	**0.855**	0.019	OU
CHDV	0.550	0.344	0.000	1.000	**0.541**	0.372	0.086	BM
CLDV	0.53	0.38	0.00007	1	0.34	**0.597**	0.06	OU
CCT1	0.430	0.73	0.00007	1.000	0.28	**0.664**	0.04	OU
CHT1	0.607	0.24	0.0001	1.000	0.337	**0.483**	0.179	OU
CLT1	0.734	0.09	0.999	0.526	**0.479**	**0.426**	0.09	BM-OU
CCT2	0.53	0.4	0.3	0.34	**0.532**	0.38	0.08	BM
CHT2	0.59	0.238	0.99	0.37	**0.384**	**0.395**	0.219	BM-OU
CLT2	0.5	0.48	0.0001	1.000	0.289	**0.663**	0.047	OU
CCT3	0.59	0.27	0.54	0.54	**0.61**	0.29	0.097	BM
CHT3	0.625	0.175	0.99	0.213	**0.461**	0.268	0.269	BM
CLT3	0.655	0.17	0.99	0.363	**0.454**	**0.412**	0.133	BM-OU
CCT4	0.42	0.78	0.00007	1	0.280	**0.67**	0.04	OU
CHT4	0.632	0.196	0.99	0.282	0.56	0.306	0.132	BM
CLT4	0.502	0.5	0.00007	1	0.394	**0.51**	0.09	OU

the Brownian Motion evolutionary model (BM), assumes that the evolution of a trait results from random fluctuations over time (Felsenstein, 1985; Harmon et al., 2010). The second model, Ornstein–Uhlenbeck (OU) model, focuses on sections of lineages in which a trait varies in relation to an optimum or stabilizing selection (Butler & King, 2004; Harmon et al., 2010). Finally, the Early Burst model (EB; Harmon et al., 2010) predicts intensified trait modifications early in the evolutionary tree followed by a gradual deceleration of the evolutionary rate. To test which evolutionary model best fits each variable, a fitContinuous analysis was run using GEIGER (Harmon et al., 2010) and APE (Analysis of Phylogenetics and Evolution; Paradis et al., 2004) packages for R. The command 'fitContinuous' describes the rate of character modification within the three aforementioned evolutionary models and provides an Akaike value (AIC) for each procedure. The best fit among the candidate evolutionary models was then obtained from the AIC (Burnham & Anderson, 2002) using the weights (wAICc) as a measure of strength for each model, which indicate the probability that a given model is the best among a series of candidate models (Burnham & Anderson, 2002).

Due to their phylogenetic relationships, species cannot be considered independent data points (Felsenstein, 1985); therefore, Pagel's phylogenetic signal (λ) was estimated using the residual errors simultaneously on the regression parameters of phylogenetic generalized least squares models (PGLS) analyses. These analyses were performed in 'caper' (Orme et al., 2012) and 'ape' (Paradis et al., 2004) packages for R. Models were built using the ecological data as the independent variable, as a proportion of locomotor modes, either individually or in combination (e.g., PC ~ bottom-walker + terrestrial-walker), and using the morphological information as the dependent variable, represented by the species' scores of each one of the four retained PCs. Model choice was based on the model fit using the AIC.

Results

Phylogenetic PCA

A phylogenetic PCA from residual values of different morphological variables (claw dataset) show that the first three

principal components (PCs) accounted for 70% of the total variance, with PC1 accounting for 50.8%, PC2 for 12.6% and PC3 for 11.5%. Loading scores and the proportion of variance for each PC are presented in Table 2. PC1 loads, which displayed negative values, show an important contribution of claw height and length of both digits and toes (Table 2). PC2 showed negative and positive values for dorsal curvature of digit V and toe IV and curvature of toe II, respectively (Table 2). PC3 showed positive values only for curvature of digits I, IV, V and toes 3 and 4.

Evolutionary Models

Claw morphology of turtles appears to have evolved through different processes, since no single evolutionary model was able to explain all the studied traits (Table 3). Most of the traits were best explained by the Ornstein–Uhlenbeck model of evolutionary change, mainly claw curvature and length of the digits and toes. The BM model better explained the evolution of the height of most claws (Table 3). Using the AIC, only one variable, claw curvature of digit 2, showed the best fit with the Early Burst evolutionary model (Table 3). Most claw traits showed a relationship with a phylogeny (λ close to 1 and not significant). However, one claw traits (CHDII) showed a λ close to 0 and significant, suggesting that variability could be a consequence of adaptation to ecological requirements.

Ecomorphological Relationships

The PGLS analysis produced 21 possible models (Supplemental Table 2). Only two of them were informative according to the Akaike criterion and provided evidence for an association between morphology and ecology (Table 4; Fig. 4). The models showed significant slopes for some of the locomotor mode variables (Table 4; Fig. 4). The bottom-walker turtles show less curved claws of digits 1, 4, and 5 of the hand and toes 1, 3, and 4 (Table 4; Fig. 4a). The freshwater turtles showed the longest and flattest claws for the same digits compared to the bottom-walker turtles (Table 4; Fig. 4b). The remaining associations were not significant (Supplemental Table 2).

Table 4 Best fitting PGLS models for PCs from morphological variables (PC1, PC2 and PC3) and locomotor modes. See Supplemental Table 2 for all possible models. Pagel's λ (phylogenetic signal), adjusted r^2 (Adj r^2), intercept, and slopes were considered for the informative variables based on the Akaike criteria (AICc and Wi). Pp: partial P value for each variable; Pt: P value for the complete model. Significant results are indicated in bold

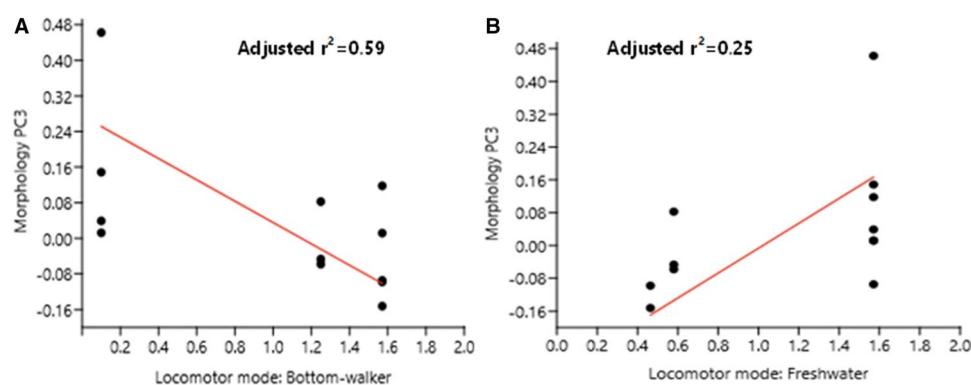| Models	λ	Adj r2	Intercept	Variable	Slope	Pp	Pt	AICc	Wi
PC3 ~ bottom-walker	0.001	0.253	0.058	Bottom-walker	− 0.117	**0.05**	**0.006**	−11.367	0.35
PC3 ~ freshwater-swimmer	0.001	0.46	0.19	Freshwater-swimmer	0.146	**0.04**	**0.008**	−10.412	0.22

Fig. 4 Product-moment relationships between and locomotor modes and morphology (principal components) according to PGLS models. Each panel shows on the x axis the locomotor modes and on the y axis (morphology) the contribution of each principal component (PC) for those relationships that were significant. Panel show **a** association between PC3 (with high contribution for curved claws of digits 1, 4, and 5 of the hand and toes 1, 3, and 4) and bottom-walker turtles; **b** the relationship between PC3 (longest and flattest claws for the 1, 4, and 5 of the hand and toes 1, 3, and 4) and the freshwater turtles. The orientation of arrows along the morphology axis indicates if the contribution of the variable increases (positive load contribution) or decreases (negative load contribution) with locomotor modes. For details see Table 4

Discussion

The anal yses of claw configuration provided an interesting perspective to propose links between claw morphological variation, ecological factors, and phylogenetic constraints. Our data show that turtles' claws exhibit highly conservative shapes, with a few variations that allow turtles to exploit all the locomotor modes daily, supporting partially our initial hypotheses. Thus, freshwater turtles' long and slightly curved claws help increase the thrust surface and walk on land, contributing to a more efficient gait (Biewener, 2003). Apart from swimming, these turtles travel long distances with slopes to access the places for nesting (Lopez et al., 2013), added to the use of the claws to tear the prey that they ingest, all activities energetically very demanding. On the contrary, terrestrial turtles' claw shapes and length are mainly explained by phylogenetic factors. The length of the claws is the most conservative variable and is highly related to terrestrial turtles. Moreover, the low variability in claw shape suggests that differences in turtle's locomotor modes are less marked than they seem. However, another explanation is also possible, that a process of many-to-one mapping, e.g., the same morphology can result in different locomotor performances, which might lead to a partial decoupling of morphological characters and function, as suggested by Wainwright et al. (2005).

Despite their main locomotor modes, all turtles can walk (López et al., 2013; Mao et al., 2013). Indeed, our quantitative analyses indicate that OU is the process that best fits most of the data. This result is in accordance with the conservative claw shape that can easily be attributed to a hierarchical evolutionary pattern. The outlines of the claws of the fossil turtles *Odontochelys*, *Proganochelys*, and the most ancestral *Pappochelys* are similar to our bottom-walker turtles (Schoch & Sues, 2019). The sediments where the fossil specimens were found indicate that the turtles came from lakes or ponds (Gaffney, 1990; Li et al., 2008; Schoch & Sues, 2018, 2019). Although they could have swum in the middle of the water column in lakes or ponds, our data indicate that they should also be considered as bottom-walkers.

Most traits exhibited low λ-values (closer to 0) of phylogenetic signal estimators but were not significant ($p > 0.005$) and precluded us from making strong statements. Some trends are, however, interesting to discuss. We recovered the same morphological pattern of long and slightly curved claws in the freshwater analyzed turtles, similar to the sand diving lizards (Tulli et al., 2009). Thus, the long and slightly curved claws could provide a better support not only in water but also on sandy substrates for sand dwellers in general (Tulli et al., 2009).

Seven of the analyzed traits fitted to a BM model, showed adaptive behavior. The height claw variable could be a useful tool to climb. Some freshwater turtles, such as species of *Phrynops*, can climb, an ability probably derived as an exaptation of its main locomotor modes (Gould and Vbra, 1982). Climbing is used to search for basking or even nesting sites on the riverbanks and floating logs (López et al., 2013).

The more ventrally curved claws of some digits of bottom-walker species could be a useful tool to assist prey capture and tearing. This feeding behavior has been observed in water-associated species, such as *Kinosternon* turtles (AM personal observations and video, Supplemental material 2) and in all water monitors, such as *Varanus mitchelli* and *V. salvator* (D'Amore et al., 2018; Schultz & Doody, 2004; Shine, 1986; Stanner, 2010). These curved claws are also used by bottom-turtles as digging tools to scratch the substrate and seem to act as more effective tools for breaking apart the substrate. Remarkably, our results suggest a leading role of digit V claw, which seems to be a specialized claw that helps to excavate refuges and unearth the mud to exit. Once again, we found that the curved claws used for scratch digging are a convergent trait in several tetrapod taxa (D'Amore et al., 2018; Schultz & Doody, 2004; Shine, 1986; Stanner, 2010; Thomson & Motani, 2021). For example, Atlantic puffins (*Fratercula arctica*) practice scratch digging with a specialized claw in their feet (Bent, 1919; Burnham et al., 2021; Hornung, 1982). Most rodents use their claws as the main digging tools, adopting a scalporial strategy (Stein, 2000). Some sigmodontinae rodents are scalporial and use their claws to scrape soil away (Tulli et al., 2016). The same scalporial claw pattern can be distinguished in the most basal turtle *Pappochelys* (Schoch & Sues, 2019), which suggests that this species could also use their claws to tear prey or as digging tools. Like other claw traits, claw ventral curvature appears linked to the same habits in different tetrapod taxa.

Our data also show several convergence traits in claw shape, with convergences being reinforced by the low phylogenetic signal exhibited by most characters. The use of claw measurements and categories based on locomotor modes allowed us to interpret turtle claw function based on morphology. We propose that claw morphology in turtles is mainly associated with some mechanical functions, such as freshwater swimming, bottom-walking and tearing of prey.

Declarations

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