Systematic Palaeontology (Vertebrate Palaeontology)

Procrustes analysis: a tool to understand shape changes of the humerus in turtles (Chelonii)

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Abstract

The aim of this paper is to study the effects of locomotor adaptations to a particular environment on the structure of an important element of the appendicular system, the humerus. The variation of the humerus shape pattern is quantified and statistically studied using geometric morphometry, from a sample of 122 humeri belonging to 69 species of extant and extinct turtles. The calculation of a multivariate regression reveals that the shape is strongly correlated with a specialization to aquatic habitat. A parallelism between shape patterns of the humerus, types of limbs coordination and aquatic strategies of life is discussed for groups of highly aquatic freshwater turtles and sea turtles. *To cite this article: M. Depecker et al., C. R. Palevol 4 (2005)*.
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Résumé

Analyse procuste : un outil pour comprendre les changements de forme de l'humérus chez les tortues (Chelonii). Le but de ce travail est d'étudier les effets des adaptations locomotrices à un environnement donné sur l'humérus, l'élément le plus proximal de la chaîne articulaire des membres des tortues. La variation du patron de forme de l'humérus est quantifiée et statistiquement étudiée par la morphométrie géométrique, à partir d'un échantillon de 122 humérus appartenant à 69 espèces de tortues actuelles et fossiles. Le calcul d'une régression multivariée montre que la conformation de l'humérus est fortement corrélée à une spécialisation au milieu aquatique. Le parallélisme entre patrons de forme de l'humérus, types de coordination des membres et stratégies de vie en milieu aquatique est discuté pour les tortues d'eau douce, grandes nageuses, et les tortues marines. *Pour citer cet article : M. Depecker et al., C. R. Palevol 4 (2005)*.
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1. Introduction

Chelonians have appeared 210 Myr ago [24]. They constitute a good example of an old well-differentiate group of organisms that has known an extensive diversification as well in numbers of lineages as in habitat use. The effects of the adaptive radiation that has occurred between 120 and 90 Myr ago [35] are still visible today. Turtles are highly diversified and occupy a large range of terrestrial and aquatic habitats all over the world (except the polar areas) [20]. Among the 240 extant species [41], some of them – most of them belonging to the family Testudinidae – are almost exclusively walkers on land, and are poor swimmers. They can live in open sandy or stony areas, when others prefer habitats like scrublands or humid undergrowths. Many other families of turtles spend time in both terrestrial and aquatic habitats, and are more polyvalent in their locomotor ability. Here again, diversity of habitat ranges from closed ponds, lakes, streams to open rivers, torrents (including shores and banks). Other species of turtles are excellent swimmers and spend little time out of fresh or sea water. That is notably the case for two families of freshwater turtles, the Trionychidae and the Carettochelyidae, which usually inhabit trouble waters of rivers, but which can also be found for some in lagoons or estuaries. The two families of extant marine turtles, the Cheloniidae and the Dermochelyidae, spend all their time in the seas and oceans of the world, the differences in the habitat concerning more or less benthic or pelagic behaviours. Among the extinct species, some like Meiolaniidae and the batagurid *Ptychogaster* are estimated to provide different patterns of terrestrial life, more primary for Meiolaniidae [11] than for *Ptychogaster* [22,25]. They could be interesting to compare with the living terrestrial species.

In spite of this extensive diversification in habitat use, turtles have maintained a relatively great stability in its basic bauplan. The main characteristic is that the trunk is encased in a rigid shell that incorporates ribs and is fused with the neural spines of the vertebrae, and so completely encloses the shoulder and the pelvic girdles. Nevertheless, other morphological traits (on shell, skull, or appendicular skeleton...) often allow distinguishing the higher categories of turtles. Those concerning the locomotor system clearly separate some families of extant turtles from others [38,40]. Although some uncertainties remain, the knowledge of phylogeny in turtles goes increasing, making the relationships within the categories of turtles more reliable [12,19,35].

In a first time, it seems interesting to examine if there are evidences for a direct relation between morphological variations of the locomotor system and diversity of habitats for the whole families of turtles. In a second time, the answer to the question how is made this link between form and habitat supposes to consider more functional aspects. The hypothesis is that the locomotor performances (but also other functional traits) depend on structural characters; associated with slight modulations of behaviour, these performances have an effect on fitness in a given habitat; this fitness corresponds to selective pressures acting back on the structural level of the organism [10].

This work consists first in distinguishing the different shape patterns of limb morphology in turtles, using a method of geometrical morphometry based on Procrustes analysis. For this preliminary study, we choose the humerus for its important motor and propulsive role in terrestrial as well as in aquatic locomotion of all categories of turtles. The purpose is secondly to test, by statistical regression, whether and how these humerus shape patterns are modified according to the different types of habitats described in turtles. At last, through lack of a real biomechanical study to directly explain the links between shape and locomotor abilities, we made a short synthesis of the principal traits of locomotor adaptations related to the different constraints imposed by the habitats.

2. Materials and methods

Two hundred and twenty-two humeri were included in the analysis. They correspond to 69 species belonging to 11 extant and 2 extinct families, respectively 114 extant and 8 extinct adult specimens (Table 1). All the specimens belong to the collections of the 'Muséum national d'histoire naturelle' of Paris, France, except for one specimen (*Carettochelys insculpta*) coming from the 'Naturhistorisches Museum' of Vienna, Austria.

Twenty-one landmarks have been chosen on the bone and have been defined according to the three levels of homology given in Bookstein [2] (Fig. 1). Six landmarks correspond to the contact of structures (type I), eight to extremities of processes (type II) and seven

Table 1

The 122 specimens studied for humerus

Tableau 1. Les 122 spécimens dont l'humérus a été étudié

Species	N	n°	Species	N	n°
Meiolaniidae			*Pyxidea mouhotii*	1	75
Meiolania platyceps	1	44	*Rhinoclemmys punctularia*	1	77
Testudinoidea			*Siebenrockiella crassicollis*	1	78
Testudinidae			**Kinosternidae**		
Astrochelys radiata	3	1, 2, 3	*Kinosternon leucostomum*	2	79, 80
Centrochelys sulcata	3	4, 5, 6	*Kinosternon subrubrum*	1	81
Chelonoidis carbonaria	4	7, 8, 9, 10	**Platysternidae**		
Chelonoidis denticulata	3	11, 12, 13	*Platysternon megacephalum*	1	82
Chersina angulata	1	14	**Chelydridae**		
Dipsochelys gigantea	3	15, 16, 17	*Chelydra serpentina*	2	83, 84
Geochelone elegans	1	18	**Chelidae**		
Homopus areolatus	2	19, 20	*Chelus fimbriatus*	2	85, 86
Indotestudo elongata	2	21, 22	*Emydura latisternum*	1	87
Kinixys belliana	1	23	*Hydromedusa tectifera*	1	88
Kinixys erosa	1	24	*Platemys platycephala*	1	89
Manouria emys	2	25, 26	**Pelomedusidae**		
Manouria impressa	1	27	*Pelomedusa subrufa*	1	90
Stigmochelys pardalis	1	28	*Pelusios castaneus*	2	91, 92
Testudo graeca	4	29, 30, 31, 32	*Pelusios gabonensis*	1	93
Testudo hermanni	1	33	*Pelusios subniger*	1	94
Testudo kleimanni	1	34	**Podocnemididae**		
Testudo marginata	2	35, 36	*Erymnochelys madagascariensis*	2	95, 96
Emydidae			*Peltocephalus dumerilianus*	1	97
Clemmys guttata	2	45, 46	*Podocnemis expansa*	1	98
Emys orbicularis	1	47	**Trionychoidea**		
Graptemys pseudogeographica	1	48	**Trionychidae**		
Malaclemys terrapin	1	49	*Amyda cartilaginea*	2	99, 100
Pseudemys rubriventris	1	50	*Apalone ferox*	1	101
Terrapene carolina	4	51, 52, 53, 54	*Aspideretes gangeticus*	1	102
Terrapene ornata	1	55	*Aspideretes hurum*	1	103
Trachemys scripta	5	56,57,58,59,60	*Cycloderma aubryi*	3	104, 105, 106
Bataguridae			*Lissemys punctata*	1	107
Ptychogaster emydoides	7	37, 38, 39, 40, 41, 42, 43	*Pelodiscus sinensis*	1	108
			Trionyx triunguis	2	109, 110
Chinemys reevesii	1	61	**Carettochelyidae**		
Cuora amboinensis	2	62, 63	*Carettochelys insculpta*	1	111
Cistoclemmys flavomarginata	1	64	**Chelonioidea**		
Geoemyda spengleri	1	65	**Cheloniidae**		
Hardella thurjii	1	66	*Caretta caretta*	3	112, 113, 114
Heosemys grandis	1	67	*Chelonia mydas*	3	115, 116, 117
Hieremys annandalii	3	68, 69, 70	*Eretmochelys imbricata*	4	118, 119, 120,121
Malayemys subtrijuga	3	71, 72, 73	**Dermochelyidae**		
Melanochelys trijuga	1	74	*Dermochelys coriacea*	1	122

Classification according to King and Burke [18],modified [3–5,19,23]. *N*: number of specimens studied; *n*: specimens represented in Fig. 2.

result from constructions (type III). The 3D coordinates of the 21 landmarks were digitized with a Microscribe (3D Revpro DX, precision of 10^{-4} mm).

After digitalization, each humerus is characterized by a set of 21 landmarks, defining a 'figure' [15]. The superimposition presupposes a size normalization of
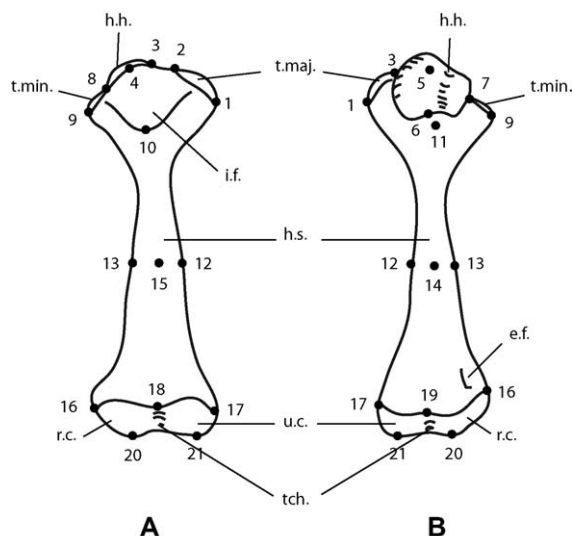
Fig. 1. Anatomy of the humerus (right side) and position of landmarks. (**A**) Ventral view. (**B**) Dorsal view. e.f., ectepicondylar foramen; h.h., humeral head; h.s., humeral shaft; i.f., intertrochanteric fossa; r.c., radial condyle; r.u., ulnar condyle; tch., trochlee; t.maj., trochanter major; t.min., trochanter minor. Landmarks 1,2, lateral and medial extremities of the trochanter major (homology I); 3,4,6,7, lateral, ventral, dorsal and medial limits of the humeral head (II); 5, geometric centre of the humeral head (III); 8,9, lateral and medial extremities of the trochanter minor (I); 10, distal limit of the intertrochanteric fossa (II); 11, maximum of curvature under the humeral head (II); 12, 13, 14, 15, lateral, medial, dorsal and ventral points of the humeral shaft at the 1/2 of the length (III); 16, 17, medial and lateral extremities of the distal epiphysis (I); 18, 19, ventral and dorsal limits between ulnar and radial condyles at the maximum of curvature (III); 20, 21, medial and lateral tops of the trochlee (II).

Fig. 1. Anatomie de l'humérus (côté droit) et position des points. (**A**) Vue ventrale. (**B**) Vue dorsale.

the 122 figures. The variable used for size normalization is the centroid size, obtained as the square root of the sum of the squared deviations of landmarks from the centre of the figure [16]. Once normalized, the 122 figures are translated and rotated to minimize distances between homologous landmarks (Generalized Least-Square criterion). A mean figure called consensus is calculated so that the shape of each humerus is then defined by a set of Procrustes residuals, which are the deviations of landmarks from the consensus. A single superimposition of all specimens was done.

The Principal Components of shape (PC) were calculated from the variance-covariance matrix of the Procrustes residuals. The principal components are new variables that extract the maximum of shape variation by decreasing order of magnitude. This step is neces-

sary because of the great number of Procrustes residuals defining each humerus (63 Procrustes residuals, that is to say 21 landmarks by 3 spatial dimensions). Lines diagrams allow visualizing the shape changes associated to the shape vectors PC1, PC2... (i.e. changes in relative positions of the 21 landmarks).

In order to determinate if the shape of the humerus can be correlated to the specialization to the aquatic habitat, we realized and tested a multivariate regression [21]. The dependent data are the PC and the independent data is a vector that corresponds to different degrees of aquatic specialization. This aquatic gradient vector was created to group together some semi-aquatic and some aquatic families, allocating to them an artificial value: 0 for Testudinidae, *Ptychogaster* and Meiolaniidae (three groups of terrestrial turtles taken as control), 1 for Emydidae, Bataguridae, Kinosternidae, Platysternidae, Chelydridae, Chelidae, Pelomedusidae, Podocnemididae, 2 for Trionychidae; 3 for *Carettochelys insculpta*; 4 for Cheloniidae; 5 for *Dermochelys coriacea*. Multivariate regression was statistically tested using the coefficient of determination (R^2) and a test F of Fisher. The calculation of the multivariate regression gives us a new shape vector, which is a linear combination of the initial shape vectors (PC): $V = a_1 \text{PC}1 + a_2 \text{PC}2 + ... + a_n \text{PC}n$. The shape changes of the humerus that are correlated with the specialization to the aquatic habitat were characterized by line diagrams.

Superimposition, statistical procedure, line diagrams and graphs were carried out with the APS software, version 2.21 [27].

3. Results

3.1. Evidence for a shape gradient of the humerus of aquatic turtles

The 122 specimens are projected onto the plane formed by the first two PC, which respectively represent 32.5 and 18.7% of total shape variance (Fig. 2; Table 2). On the left of the graph are located most of the families of terrestrial and freshwater turtles. For more details, group A corresponds to the extant terrestrial Testudinidae, and the extinct terrestrial *Ptychogaster*; group B to the semi-aquatic Emydidae, Bataguridae, Kinosternidae, Platysternidae, Chelydridae,
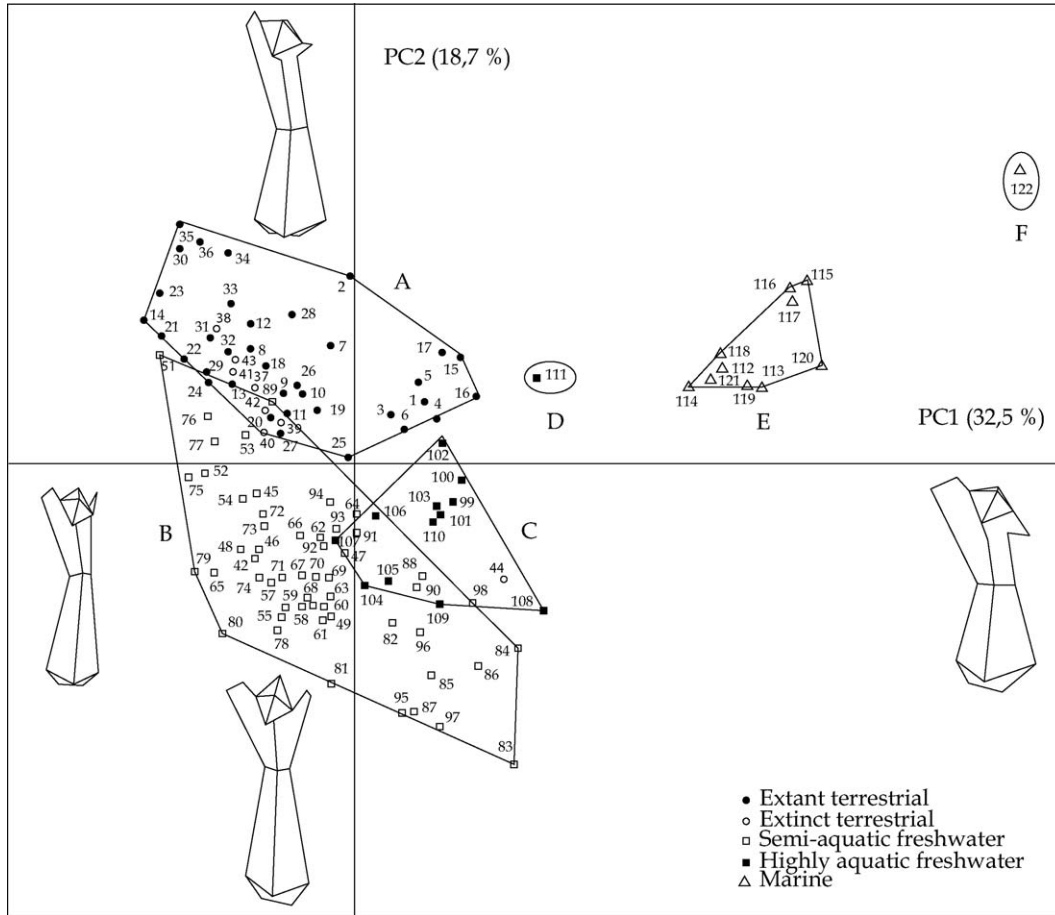
Fig. 2. Principal component analysis of the 122 humerus. Group A: Testudinidae, *Ptychogaster*; group B: Emydidae, Bataguridae, Kinosterni-dae, Platysternidae, Chelydridae, Chelidae, Pelomedusidae, Podocnemididae; group C: Trionychidae, Meiolaniidae; group D: Carettochelyidae; group E: Cheloniidae; group F: Dermochelyidae. Dorsal views of line diagrams of the humerus for the two extremities of PC1 and PC2.
Fig. 2. Analyse en composantes principales des 122 humérus.

Table 2
Statistics for the PCA and the multivariate regression
Tableau 2. Statistiques pour l'ACP et la régression multivariée

Numbers of PC included	*% of total shape variance*	*Cumulated %*	R^2	F	Degrees of freedom	Probability p
1	*32.5*	*32.5*	0.64	215	1, 120	$< 10^{-6}$
2	*18.7*	*51.2*	0.68	126	2, 119	$< 10^{-6}$
3	*9.0*	*60.2*	0.73	108	3, 118	$< 10^{-6}$
4	*6.9*	*67.1*	0.74	85	4, 117	$< 10^{-6}$
5	*5.5*	*72.6*	0.75	70	5, 116	$< 10^{-6}$
6	*3.7*	*76.3*	0.75	58	6, 115	$< 10^{-6}$
7	*3.1*	*79.4*	0.79	62	7, 114	$< 10^{-6}$
8	*2.3*	*81.7*	0.81	61	8, 113	$< 10^{-6}$

Chelidae, Pelomedusidae and Podocnemididae; group C to the extant potentially highly aquatic Trionychidae and the specimen of extinct terrestrial Meiolaniidae. Group D corresponds to the single specimen of the potentially highly aquatic freshwater turtle, *Carettochelys insculpta*. Group E includes all the species of the marine Cheloniidae. Group F represents a single specimen of the highly marine turtle, *Dermochelys coriacea*. We observe an orientation in the different shape patterns of the humerus, which seems to be related to groups of turtles more and more aquatic-adapted, according to a gradient from complex habitats (group B in ponds, lakes and more or less small rivers and also quiet estuaries), intermediate habitats (groups C and D in large rivers and estuaries with strong streams) to open habitats (groups E and F in seas and oceans). The shape changes in the humerus pattern associated with PC1 principally concern the width of the bone, which increase for the more aquatic groups of turtles. Those associated with PC2 correspond to trochanters, which become more or less symmetric when going from one extremity to another extremity of the shape vector.

3.2. Shape of humerus and aquatic habitats

A multivariate regression was performed to calculate the degree of correlation between the humerus shape and the degree of specialization to aquatic habitat (Fig. 3). Such a multivariate regression extracts more information than with classical regression using each principal component separately. The test of the multivariate regression was more significant with seven PCs only than with all the PCs (Table 2). The vector calculated with the first seven PCs (79.4% of total shape variance) is:

V = 0.97 PC1 – 0.18 PC2 – 0.17 PC3 – 0.06 PC4 + 0.04 PC5 – 0.001 PC6 – 0.07 PC7

However, graphic results are the same with all the PCs. We note in Fig. 3 that the shape differences between the terrestrial (group A) and the semi-aquatic turtles (group B) are few, and that the differentiation of humerus shape increases according to more and more aquatic turtles (groups C, D, E, F).

The line diagrams of shape changes associated to V show that, when going from terrestrial and semi-
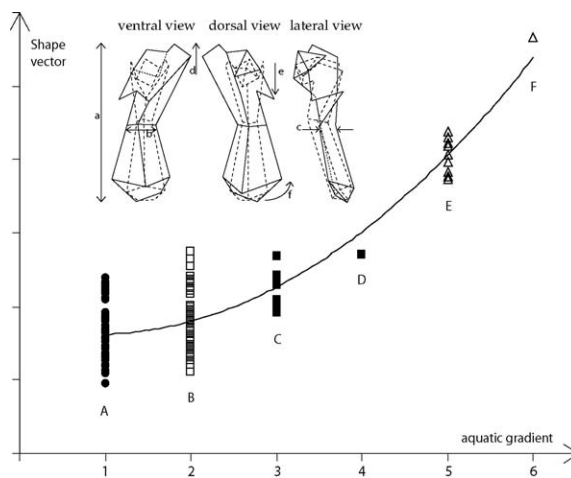

Fig. 3. Correlation between shape changes of the humerus (Vreg) and specialization to the aquatic habitat (aquatic gradient). Line regression: $y = 0.0144 x^2 + 0.0032 x – 0.0377$; $R^2 = 0.81$. Symbols are the same as in Fig. 2. Ventral, dorsal and lateral views of line diagrams of the humerus between both extremities of Vreg: dashed lines, semi-aquatic turtles; full lines, marine turtles. Shape changes observed: a, longer humerus; b, larger shaft; c, flatter shaft; d, developed trochanter major; e, distal trochanter minor; f, enlarged radial condyle.
Fig. 3. Corrélation entre les changements de forme de l'humérus (Vreg) et la spécialisation à l'habitat aquatique (gradient aquatique). Régression linéaire : $y = 0.0144 x^2 + 0.0032 x – 0.0377$; $R^2 = 0.81$. Les symboles sont les mêmes que sur la Fig. 2.

aquatic turtles (groups A and B) to more aquatic turtles (groups C and D), until marine turtles (groups E and F), the humerus becomes more robust relatively to the length (a) (Fig. 3). Its shaft becomes larger (b) and dorso-ventrally flatter (c). The *trochanter major* (or medial process) is proximally developed (d), whereas the *trochanter minor* (or lateral process) has moved distally (e). The radial condyle is laterally enlarged (f).

4. Discussion

The results show that changes in humerus shape is correlated to aquatic and particularly marine adaptation. Concerning the terrestrial habitat, we observe that the specimens belonging to two related families Testudinidae and *Ptychogaster* [22,25] have similar humerus structure, whereas the specimen belonging to the non-related family Meiolaniidae [11,28,29] possesses a totally different humerus shape (Fig. 2). This suggests two different ways of terrestrial adaptation, knowing that the terrestriality of the Meiolaniidae provides from

a primary adaptation whereas the Testudinidae [24] and *Ptychogaster* have secondarily returned to a terrestrial lifestyle from freshwater forms. A more detailed study concerning evolution of terrestriality in turtles related to the locomotor system should constitute an interesting way of investigations. In our study, the differentiation of the humerus shape pattern is much more marked when considering adaptation to the aquatic habitats.

Humerus shape seems to be directly related to a range of peculiar constraints corresponding to specific environments.

4.1. How explain such a greater influence of the aquatic environment on humerus structure, compared to the terrestrial environment?

The constraints that are related to the locomotor function and influence the fitness of turtles in a given habitat may be more various in water than on land.

4.1.1. Behavioural constraints

In vertebrates, the change to terrestrial life in evolution was very profound to build a well-adapted 'machine'. However, we can estimate that the reverse trend back to water was 'easier' and 'faster', occurring many times, especially in chelonians [12,35]. These secondary swimmers may have found some advantages in regard to the non-swimmers: new favourable possibilities for dispersal and migration, new access to food. They may also escape terrestrial predators and may play the role of new predators themselves. These various behavioural characteristics required from turtles a new field of locomotor performance: speed and endurance, diving, new systems for acceleration and manoeuvrability.

4.1.2. Physical constraints

The terrestrial habitat is not very homogeneous; however the weight – because of gravity – is the main physical constraint. The heavy body which is unfavourable to progress on land becomes an indifferent factor in water. However, new and various physical constraints appear, related to the important diversity of aquatic habitats mentioned in introduction (ponds, lakes, rivers, torrents, estuaries, seas...). Every kind of aquatic environment possesses its characteristics of salinity, pressures, current..., which imposed a new range of locomotor constraints. The density and viscosity of the

water may oppose a great resistance to the motion of the body. Turtles must reduce this water resistance and propel themselves in this relatively dense environment with different systems of force exchange. They must also control their position and body equilibrium. The aquatic life also implies other adaptations like control of body temperature, modification in respiratory and circulatory physiology, protection of new organs...

4.2. Is it possible to relate some main functional aspects of the terrestrial and aquatic locomotion with some structural traits described for the humerus pattern?

Roles and implicated movements of the humerus vary with the different locomotor functions used by living turtles when walking or swimming in different habitats.

4.2.1. Typical walkers

When walking on land, most of terrestrial and freshwater turtles, and some hatchlings of marine turtles use alternate movements of their four limbs, which generally corresponds to a walk or a trotted walk, based on the lateral sequence [18,36,39,40]. In this case, the humerus is alternatively protracted and retracted, and slightly rotated about its longitudinal axis [36]. Because the body and the proximal part of the limbs are encased in a voluminous shell, the humerus may be longer in walking turtles like Testudinidae to increase its protaction and retraction in the horizontal plane. In the same way, the humerus shaft may be arched to facilitate the rotation of the bone about its longitudinal axis.

4.2.2. Typical swimmers

When swimming or walking at the bottom of water, turtles usually use alternate movements of their four limbs, but opposite to walking, the gait is based on the diagonal sequence [9,30,33,39,40]. As for terrestrial locomotion using alternate coordination, the swim by paddling is characterized by succession of protraction and retraction of the humerus in a more or less horizontal plane [26]. Compared to the great number of species of turtles that are able to swim, only a few number of highly aquatic turtles can swim in fresh- or seawaters using simultaneous movements of fore- or hindlimbs or the both together. It concerns a single species of freshwater turtles, *Carettochelys insculpta* [6,13,26,

39,41], and the seven species of extant marine turtles, corresponding to the six genera *Caretta*, *Chelonia*, *Dermochelys*, *Eretmochelys*, *Lepidochelys*, and *Natator*. During synchronous swimming, the motor pattern of the humerus corresponds to predominant vertical movements that follow upstroke and downstroke of the forelimbs [7,9,30–34,37,39]. The forelimbs of highly aquatic turtles have evolved to increase the efficiency of these flapping movements. The limbs that propel the body present a flat and extended surface to the water on the most of the power stroke (i.e. the downstroke). To reduce the drag, their web-footed limbs are flexed and their fingers and toes adducted on the beginning of the recovery stroke (i.e. the upstroke) [31,33]. The distal part of the limb is thus lengthened, while the proximal part, and so the humerus is flattened and shortened to increase the thrust against the water. In spite of this aquatic adaptation, highly aquatic turtles stay basically terrestrial forms that still have an aerial respiration like the other turtles and have to come back to the land for reproduction. Marine adult turtles that return to the sand to nest, and hatchlings of leatherback turtles that leave the nest to reach the sea both use their peculiar transformed limbs in another type of terrestrial locomotion than the typical terrestrial forms. It consists of the use of cyclic and synchronous movements of the fore- and hindlimbs. This functional pattern permits to adult turtles to produce efficient and energetic-saving propulsion on the land, despite the increasing of their body weight. Forward propulsion is mainly assumed by simultaneous movements of the forepaddles, using them as if they were walking on crutches [31–34]. The humerus is protracted and retracted into a more inclined plane than for usual alternative walk [32].

4.3. What are the relationships between structural, functional and behavioural gradients?

4.3.1. Increase of propulsive efficiency by the development of foreflippers

In highly aquatic turtles, the propulsive force is mainly generated by the forelimbs, overall during the downstroke but also during the upstroke of the locomotor cycle [9]. This is partly due to the wing-like hypertrophied forelimbs. In young marine turtles, *Chelonia mydas*, the surface area of the foreflippers is twice that of the hindlimbs; whereas in other freshwater turtles, the surface areas of the fore- and hindlimbs are either quite similar or it is the hindlimb that is a little bigger [9]. Considering the relative length of the foreflippers, Renous [31] has noticed that the ratio 'forelimb length/total body length' increases for turtles more and more specialized to open aquatic habitats. The shape of the humerus is modified according to the same gradient, becoming longer, robust and flatter in the most aquatic and marine forms than in the semi-aquatic freshwater forms, as the forelimb becomes a real natatory forepaddle, longer, larger and flatter.

4.3.2. Increase of propulsive efficiency by the use of a synchronous coordination of the limbs progressively replacing the alternate pattern

From a mechanical point of view, the paddles thrust in a direction nearly opposite to the forward motion of the body. In diagonal coordination, since the thrust is applied beside, a torque is established that tends to turn the head toward the opposite side. This torque must be countered by the stroke of a paddle on the other side of the body. For this reason, the better swimmers have the paddles of the two sides of the body placed directly opposite to one another and they usually use them simultaneously. The gradient of efficiency goes in the direction where the diagonal pattern is progressively replaced by the synchronous pattern. The pitted-shelled turtle *Carettochelys insculpta* usually walks and swims using alternate coordination of the four limbs, like other terrestrial and freshwater turtles do. However, it is the only known freshwater turtle whose adults and juveniles can sometimes swim using synchronous movements of hypertrophied flapping forelimbs [6,13,26,39]. At low speeds, the young loggerhead turtles *Caretta caretta* swim using simultaneous beating of their hindlimbs [8]. The adults use synchronous movements of their four limbs, like the other adult marine turtles do, but occasionally still practice an alternate paddling of the four limbs [34]. All the hatchlings of Cheloniidae reach the sea using an alternate walk of the four limbs. Finally, whatever age or speed, terrestrial and aquatic locomotion, the displacement of the leatherback turtles *Dermochelys coriacea* always results from the synchronous use of the forelimbs, which are the true propulsive organs [30–34]. The movements of the hindlimbs are synchronous with those of the forelimbs, but provide a reduced propulsive force in terrestrial locomotion and act more as rudders in aquatic locomotion [31,34,37].

4.3.3. The importance of life strategies in aquatic adaptation

These strategies [17] constitute an ecological range that coincides with the morphological and functional ranges described above. The loggerhead turtles are the most neritic marine turtles, and a transatlantic travel of a juvenile as reported by Eckert and Martins [31] must be relatively exceptional. Hawksbill and green turtles also usually live on continental shelves and island coasts, but more frequently effectuate energetic-expensive migrations by sea to reach nesting beaches. Last, the leatherback turtles are the well-adapted turtles to a true pelagic life, being able to migrate over very long distances through water as well as to dive to very great depths [8]. Concerning the fly-river turtles *Carettochelys insculpta*, it occurs in rivers (including estuarine reaches and river deltas), grassy lagoons and lakes of Papua New Guinea, Irian Jaya (Indonesia) and in top part of the Northern Territory in Australia. There are no sub-specific differentiation between the two populations of Papua New Guinea and Australia, the population of Australia probably providing from a recent invasion from New Guinea [14]. According to the time of this event, *Carettochelys* could effectuate a long travel across the sea. Some authors suppose permanent exchanges between both the Australian and the Guinean populations [1].

4.4. Conclusion

We have seen that humerus shape pattern is very variable, and that these variations range from generalist to very aquatic-specialist turtles. This shape specialization of the humerus participates in the functional adaptation of the forelimb to the new constraints related to life in wide open environment like seas and oceans. It also illustrates the importance of functions such as locomotion in evolution of structures such as the appendicular system. It is notably clear if we compare the two categories of great swimmers turtles: the highly swimming freshwater forms (Carettochelyidae) to the non-related marine forms (Cheloniidae and Dermochelyidae), which show remarkable convergences of their locomotor system, included at the structural level with similar specializations of the humerus. On the contrary, the same function (i.e. adaptation to terrestrial locomotion) does not imply necessarily the same evolution in the structure of all the parts of a body, as sug-

gested by the difference in the shape of the humerus of the two non-related extinct terrestrial families, *Ptychogaster* and Meiolaniidae.

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