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ORIGINAL PAPER

Changing Modular Patterns in the Carnivoran Pelvic Girdle

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Abstract

Patterns of phenotypic integration and modularity provide important clues to understand phenotypic evolution. Here, we investigate patterns of integration and modularity of the pelvic girdle in mammalian carnivorans. Three-dimensional geometric morphometrics was used to test for different modular hypotheses by combining in different ways the four original girdle elements (i.e., ilium, ischium, pubis, and acetabulum). These hypotheses were tested with the complete sample (i.e., order Carnivora) and within families. The hypotheses with more statistical support recognize the four girdle elements as separate modules, with the ischium and pubis more integrated than the ilium and acetabulum. This indicates a strong influence of developmental units in shaping pelvic anatomy. Strikingly, the families Canidae and Ursidae exhibit a different pattern of modularity, showing a modification of the pattern displayed by the whole order, which was attained early in the evolution of the group. Our results indicate that, on long timescales, evolution can change the relationships between structures independently of the developmental patterning, thus overcoming evolutionary constraints.

Keywords Pelvis · Modularity · Carnivorans · Evolution · Development · Natural selection · Geometric morphometrics

Introduction

Phenotypic evolution is largely influenced by covariation between morphological traits, as this covariation can lead to internal constraints or can facilitate evolutionary paths (Goswami et al. 2014). This covariation (or integration) is originated by trait interactions at different levels –e.g., genetic (e.g., Mezey et al. 2000; Pavlicev et al. 2008), developmental (e.g., Cheverud 1996), or functional (e.g., Martín-Serra et al. 2015)– that could interplay in a rather complex way (Hallgrímsson et al. 2009). Therefore, the study of integration and how this integration is structured (modularity) can provide important clues about how these aspects influence and constrain phenotypic evolution. For this reason, integration and modularity have been in the last few decades the object of many studies from an evolutionary point of view (e.g., see Olson and Miller 1951, 1958; Van Valen 1965; Cheverud 1996; Wagner and Altenberg 1996; Klingenberg and Zaklan 2000; Marroig and Cheverud 2001; Magwene 2001; Hansen 2003; Goswami 2006a; Young and Badyaev 2006; Wagner et al. 2007; Hallgrímsson et al. 2009; Goswami and Polly 2010a, b; Klingenberg 2010, 2014; Bell et al. 2011; Bennett and Goswami 2011; Porto et al. 2013; Goswami et al. 2014; Martín-Serra et al. 2015; Melo and Marroig 2015; Hanot et al. 2017, 2018).

Those structures formed by several bones are of particular interest for the study of modularity. This could be the case of the vertebrate skull or the pelvic girdle, because the interplay between the developmental origin of their bone constituents and their shared functions is conspicuous. However, while the modularity of the skull has been the object of several studies (e.g., see Goswami 2006a, b for mammals; Sanger et al. 2012 for lizards; Felice and Goswami 2017 for birds), the modularity of the pelvic girdle has been comparatively less studied.

In the case of mammals, each half of the pelvic girdle is called the innominate bone, which is formed by three fused bones: ilium, ischium, and pubis. These three bones converge in the acetabulum, which is the articular surface for the joint of the pelvic girdle with the femoral head (Polly 2007). Developmental studies performed on the mammalian pelvis

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indicate that each bone is formed separately by one center of ossification, and that the ilium starts its ossification before the ischium and pubis, both starting at the same time (Pomikal and Streicher 2010). On the other hand, the morphogenesis of the acetabulum takes place in close association with the femoral head and without this contact the acetabulum cannot develop a normal shape (Harrison 1961; Pomikal and Streicher 2010). This means that the curvature of this joint surface is not genetically determined but results from a process of "epigenetic coaptation," generated as a mechanical reaction to the friction of the femoral head with the girdle bones during the early stages of development. This knowledge on the development of the pelvic girdle makes it an appropriate model for the study of patterns of integration and modularity among its bone elements, as happens with the skull.

In this study, we explore the patterns of modularity in the pelvic girdle of large carnivorans (Carnivora, Mammalia). Mammalian carnivorans are an excellent choice, as they exhibit high ecological and morphological variability regarding locomotor habits and limb bones (e.g., Van Valkenburgh 1985, 1987; Taylor 1989; Samuels et al. 2013; Martín-Serra et al. 2014a, b). Moreover, the pattern of phenotypic variability of the carnivoran pelvic girdle is very different from that of the remaining major limb bones (i.e., scapula, femur, tibia, humerus, radius, and ulna), as it seems to be more influenced by phylogeny than the others. This was evidenced in the phylomorphospaces performed by Martín-Serra et al. (2014b), which showed that, contrary to other major limb bones, each carnivoran family occupied a well-delimited portion of the pelvis morphospace. Furthermore, the pattern of integration of the pelvic girdle differs from those of other major limb bones, because the pelvis (considered as a unit) is weakly integrated with other limb elements, such as the femur and the pectoral girdle, while these elements are strongly integrated among them (Martín-Serra et al. 2015).

Material and Methods

Sample and Geometric Morphometrics

The dataset comprises 128 innominate bones (or half-pelvises) belonging to 46 living carnivoran species (Table 1). Only adult specimens were included, as indicated by complete fusion of pelvic growth plates. All specimens included in this study are housed at the American Museum of Natural History, New York, and the Natural History Museum, London (AMNH and NHM; see Table S1).

We digitized a series of 3D-landmarks onto each innominate bone using a Microscribe G2X (Inmersion Corporation). The landmarks were selected to capture the most important aspects of pelvic shape (Fig. 1a and Table S2).

We aligned the raw coordinates of the landmarks using a Procrustes fit (Dryden and Mardia 1998) to remove the effects of rotation, translation, and scaling (Rohlf and Marcus 1993). Afterwards, the Procrustes coordinates and centroid sizes (a proxy for size) were averaged by species. This procedure was performed in MorphoJ software package (Klingenberg 2011). Afterwards, this dataset was imported into R environment (R Core Team 2017) for subsequent analyses.

To quantify the presence of phylogenetic signal in the shape and size relationships, we assembled a phylogeny of the species analyzed following published sources (Koepfli et al. 2007; Nyakatura and Bininda-Emonds 2012) using Mesquite (Maddison and Maddison 2011). Then, we performed a phylogenetic Procrustes ANOVA using the function *procD.pgls* (Adams and Collyer 2015) of the *geomorph* package (Adams and Otárola-Castillo 2013), where Procrustes coordinates were the dependent variables and the log-transformed centroid size was the independent variable under a phylogenetic background. This method provided allometric corrected residuals. Then we analyzed two different datasets: (i) a dataset with the Procrustes coordinates of the species averages; and (ii) a dataset with the non-allometric residuals obtained from the phylogenetic Procrustes ANOVA.

Finally, we performed one principal components analysis (PCA) on each dataset to explore its structure of morphological variation and to detect possible outliers.

Detecting Patterns of Modularity

In order to analyze patterns of modularity in the pelvis, the innominate bone was divided into four basic elements based on their developmental origin: ilium, ischium, pubis, and acetabulum. The first three elements correspond with the three fused bones that form the innominate bone (Kardong 2006). In contrast, the acetabulum has been considered as an independent element because it develops in close association with the femoral head (Pomikal and Streicher 2010), as explained above. Subsequently, each landmark located on the innominate bone was assigned to one of these basic elements (Fig. 1b).

All hypotheses of modularity (partitions) that resulted from the possible combinations of these four elements were tested separately: one with four modules (one per element, 1/1/1/1), six with three modules (e.g., 1/1/2) and seven with two modules (e.g., 2/2 and 1/3).

To perform the modularity tests, we calculated the average covariance ratio coefficient (CR; Adams 2016) for each modular hypothesis, and we used the function *modularity.test* (Adams 2016) of the *geomorph* package (Adams and Otárola-Castillo 2013). The CR coefficient, which is independent of sample size, provides an estimation of the strength of the integration between the modules (for a detailed description of this coefficient, see Adams 2016). Afterwards, the significance of each CR coefficient was evaluated with 999

Table 1 Species of mammalian carnivorans included in this study (N: number of specimens analyzed) classified by family. For additional details, see Table S1

Family	Species	N	Family	Species	N
Ailuridae	*Ailurus fulgens*	2	Felidae	*Panthera tigris*	4
Canidae	*Canis adustus*	1		*Puma concolor*	4
	Canis aureus	2		*Uncia uncia*	4
	Canis latrans	5		Total	36
	Canis lupus	5	Hyaenidae	*Crocuta crocuta*	5
	Canis mesomelas	4		*Hyaena brunnea*	1
	Canis simensis	1		*Hyaena hyaena*	2
	Cerdocyon thous	5		Total	8
	Chrysocyon brachyurus	2	Mustelidae	*Eira barbara*	2
	Cuon alpinus	4		*Lontra canadensis*	2
	Lycaon pictus	2		*Meles meles*	1
	Nyctereutes procyonoides	2		Total	5
	Otocyon megalotis	2	Procyonidae	*Bassariscus astutus*	1
	Speothos venaticus	2		*Nasua nasua*	1
	Urocyon cinereoargenteus	4		*Potos flavus*	3
	Vulpes lagopus	2		*Procyon lotor*	3
	Vulpes velox	2		Total	8
	Vulpes vulpes	3	Ursidae	*Ailuropoda melanoleuca*	4
	Total	48		*Helarctos malayanus*	1
Felidae	*Acinonyx jubatus*	5		*Melursus ursinus*	3
	Leptailurus serval	1		*Tremarctos ornatus*	1
	Lynx rufus	4		*Ursus americanus*	3
	Neofelis nebulosa	1		*Ursus arctos*	4
	Panthera leo	5		*Ursus maritimus*	2
	Panthera onca	3		*Ursus thibetanus*	3
	Panthera pardus	5		Total	21

permutations of random partitions by changing the assignation of the landmarks within the modules (Adams 2016). Then, the proportion of random partitions with CR coefficients that are smaller than or equal to the value for the tested hypothesis indicates its statistical significance. It is worth mentioning that we selected a $\alpha = 0.01$ confidence limit rather than the usual 0.05 threshold for avoiding an overload of partially significant hypotheses. We also performed a bootstrapping test to calculate confidence intervals for the CR coefficients implemented in the function *modularity.test* of the *geomorph* package of R (Adams and Otárola-Castillo 2013).

We also analyzed separately patterns of modularity for the following three families: Felidae, Canidae, and Ursidae. We chose only these families because they were the ones with higher number of specimens sampled (i.e., 36, 48, and 21, respectively). However, given that the number of species per family was not high, in these analyses, we did not average specimens per species. For these restricted samples, we performed a set of new Procrustes ANOVAs to test for allometric effects, using *procD.lm* (Collyer et al. 2015) function of *geomorph* package (Adams and Otárola-Castillo 2013). Procrustes coordinates were introduced as the dependent variables and log-tranformed centroid size as the independent variable. In those cases that proved significant, we used the residuals in modularity tests instead of the Procrustes coordinates. The modularity tests were conducted following the same procedure as for the whole order (see above).

All the raw coordinates data analyzed during this study are included in the supplementary information (Suppl. info. – Dataset).

Results

Modularity for the Whole Order Carnivora

Given that the phylogenetic Procrustes ANOVA yielded significant results for the allometric shape change (Table S3), we performed the analysis using the allometric residuals to investigate those patterns of modularity that are free of allometric effects.

The PCAs performed from the Procrustes coordinates and the non-allometric residuals show that the species are evenly distributed along the axes (Fig. 2a, b). In addition, the

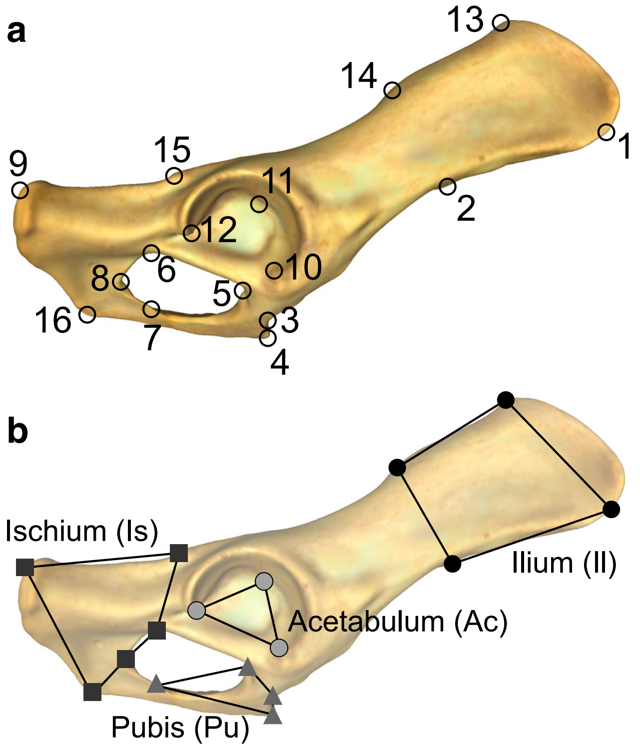

Fig. 1 Three-dimensional landmarks and developmental elements of the pelvic girdle of carnivorans. **a**, Location of the 3D-anatomical landmarks digitized on the half-pelvis. **b**, developmental elements in which the half-pelvis has been divided for the modularity tests

morphospaces are very similar between these two datasets. Accordingly, the results of the modularity tests were also very similar (Table 2). The first hypothesis –four modules– was statistically significant (Table 2), which suggests that each basic element represents an independent module. Among the hypotheses of 'three modules', several combinations of elements were significant (Table 2). However, among the two-modules hypotheses, only three of them were significant: (i) ilium + acetabulum / ischium + pubis, (ii) ilium / ischium + pubis + acetabulum, and (iii) acetabulum / ilium + ischium + pubis (Table 2).

Modularity within Families

The results of the allometric Procrustes ANOVAs performed separately for each family were statistically significant in the case of Felidae and Canidae, but not for Ursidae (Table S4). Therefore, we performed subsequent analyses from allometric residuals for the families Canidae and Felidae, and from Procrustes coordinates for the family Ursidae.

The modularity tests for the families Canidae and Felidae yielded similar results as the ones for the three families analyzed of the order Carnivora (Tables 2 and 3). However, the results for the family Ursidae provided less significant modular hypotheses than the previous ones, as only those that considered the acetabulum as an independent module were significant (Table 3). In addition, the pelvis of ursids shows, in general, the greatest CR coefficients of the three families and, in many cases, this difference is statistically significant as the confidence intervals obtained with the bootstrapping procedure do not overlap between ursids and the other families (Table 3).

Discussion

The substantial amount of significant modularity hypotheses obtained here does not have to be interpreted as mutually exclusive. In contrast, modules may be organized hierarchically, as the degree of covariation among them can also vary. For example, even if the ischium, ilium, and pubis are three separate modules, the ischium and pubis could covariate more closely between them than with the ilium, so the hypothesis of an association between the ischium and pubis would also be significant. Therefore, the different significant hypotheses obtained here should be interpreted together as the outcome of a general pattern, instead of looking for a single and most probable hypothesis that may not reflect the complexity of the pelvic girdle.

Starting from the higher number of modules, the modularity tests for all carnivorans indicate that four independent modules shape the pelvis of carnivorans. As these modules correspond with the four constituting bone elements (Kardong 2006; Pomikal and Streicher 2010), a strong developmental influence in shaping the integration pattern of the carnivoran pelvic girdle is deduced.

The relatively high number of significant hypotheses of three and four modules indicates that the modular pattern of the carnivoran pelvis is more complex than previously expected. However, they suggest a closer association between the ischium and pubis. According to the study of Pomikal and Streicher (2010) on the development of the pelvic girdle in the mouse, this association between the modules could respond to developmental timing, as the ilium seems to be more independent and is the first to start its ossification. In contrast, the ischium and pubis are more closely associated and start their ossification in the mouse at the same time after the ilium. This developmental influence in the pelvis phenotype may be related to the strong phylogenetic signal in the phenotypic variability of the pelvis (see Fig. 2), in contrast with the other major limb bones (Martín-Serra et al. 2014a, b, 2015).

We also explored the within-families modular pattern for the three families with high sample size: Felidae, Canidae, and Ursidae. The pelvic girdle of the family Ursidae is more strongly integrated than the ones of Felidae and Canidae, as indicated by their greater CR coefficient values. Regarding the modular patterns, the four basic elements (i.e., ilium, ischum, pubis, and acetabulum) are four modules for the three families, as they are for all carnivorans. However, the results of the modularity tests also show that the relationships between these

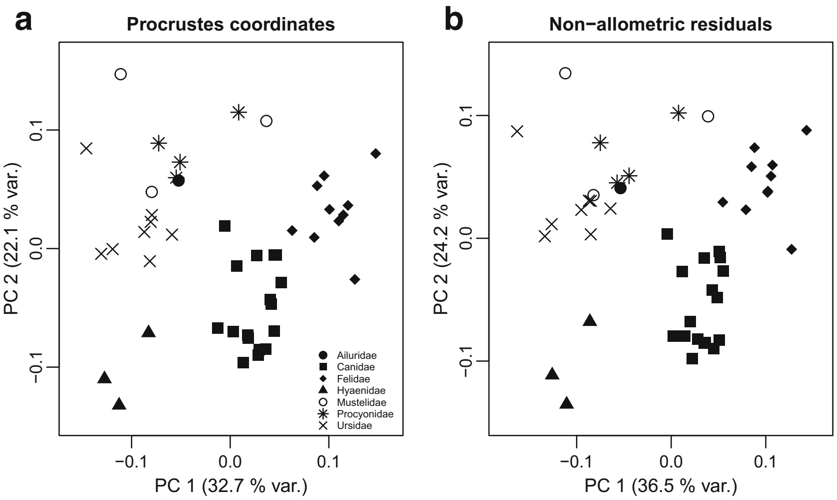

Fig. 2 Results of principal components analyses. **a**, bivariate plot of the first two PCs obtained in the PCA computed from the Procrustes coordinates. **b**, bivariate plot of the first two PCs obtained in the PCA computed from the non-allometric residuals (see text for details)

modules are different for each family. First, the modularity tests in ursids clearly indicate that the ilium, ischium, and pubis are strongly integrated with each other, whereas the acetabulum is the most independent element. In contrast, the modular pattern of the family Felidae is different, as the ischium and pubis are more strongly integrated with each other than with the ilium or the acetabulum. This indicates that the morphological evolution of the pelvis in Felidae may also have been influenced by development, as the ischium and pubis share a similar timing during ontogeny (Pomikal and Streicher 2010). The family Canidae shows an intermediate modular pattern between those of ursids and felids, as the hypothesis that associates the ilium, ischium, and pubis is significant but the ones that keep the ilium as an independent module are also partially significant.

According to these results, at least ursids and canids show that different developmental elements can evolve coordinately despite their original developmental disassociation. Therefore, the results shown here suggest that a number of changes in the modular structure of the pelvic girdle took place early in the evolution of the order Carnivora, when the families diverged, acquiring each lineage a unique pelvic morphology (Martín-Serra et al. 2014b) with a particular modular pattern.

In summary, the pelvic girdle represents a remarkable example of how phenotypic evolution can override and modify the developmental patterns of modularity inherited from an ancestor. These results add a new perspective to previous work that found changes in the patterns of integration in the mammalian appendicular skeleton (Young and Hallgrímsson 2005; Martín-Serra et al. 2015; Hanot et al. 2017, 2018), as they involve changes in the modular pattern in addition to changes in the strength of integration. Moreover, our results suggest a 'one-to-many mapping' pattern for the pelvic girdle of carnivorans, which seems to be organized in a more labile way than other complex structures of the vertebrate skeleton, such as the skull. For example, as noted by Figueirido et al. (2011), skull shape

Table 2 Results of the CR values calculated for each modularity hypothesis performed with the whole sample of the order Carnivora. Abbreviations: Il, illium; Is, ischium; Pu, pubis; Ac, acetabulum. Statistical significance of the permutation test is indicated for α 0.01 (**) and 0.05 (*). CI, bootstrap confidence intervals

		Procrustes coor. (CI)		Non-allometric res. (CI)	
4 modules	Il/Is/Pu/Ac	0.781**	(0.754, 0.891)	0.784**	(0.768, 0.889)
3 modules	Il/Is/Pu + Ac	0.833**	(0.786, 0.963)	0.812**	(0.772, 0.945)
	Il/Is+Ac/Pu	0.788**	(0.736, 0.926)	0.806**	(0.750, 0.942)
	Il + Ac/Is/Pu	0.893*	(0.859, 0.987)	0.918	(0.877, 1.013)
	Il/Is+Pu/Ac	0.675**	(0.630, 0.841)	0.648**	(0.630, 0.792)
	Il + Pu/Is/Ac	0.887*	(0.826, 0.990)	0.885*	(0.828, 0.981)
	Il + Is/Pu/Ac	0.776**	(0.713, 0.897)	0.791**	(0.735, 0.918)
2 modules	Il + Is/Pu + Ac	0.832*	(0.740, 0.982)	0.832*	(0.739, 0.986)
	Il + Pu/Is+Ac	1.008	(0.932, 1.098)	1.014	(0.940, 1.095)
	Il + Ac/Is+Pu	0.758**	(0.705, 0.910)	0.778**	(0.723, 0.912)
	Il/Is+Pu + Ac	0.675**	(0.595, 0.876)	0.653**	(0.588, 0.839)
	Is/Il + Pu + Ac	1.081	(1.031, 1.131)	1.074	(1.022, 1.123)
	Pu/Il + Is+Ac	0.858*	(0.770, 0.981)	0.919	(0.818, 1.046)
	Ac/Il + Is+Pu	0.757**	(0.662, 0.909)	0.761**	(0.676, 0.909)

Table 3 Results of the CR values calculated for each modularity hypothesis performed separately in the families Felidae, Canidae and Ursidae. Abbreviations: Il, illium; Is, ischium; Pu, pubis; Ac, acetabulum. Statistical significance of the permutation test is indicated for α 0.01 (**) and 0.05 (*). CI, bootstrap confidence intervals

		Canidae (CI)		Felidae (CI)		Ursidae (CI)	
4 modules	Il/Is/Pu/Ac	0.821**	(0.805, 0.931)	0.780**	(0.770, 0.908)	1.012**	(0.939, 1.128)
3 modules	Il/Is/Pu + Ac	0.904**	(0.858, 0.989)	0.856**	(0.842, 0.953)	1.096	(1.025, 1.149)
	Il/Is+Ac/Pu	0.908*	(0.856, 0.996)	0.802**	(0.783, 0.910)	1.110	(1.029, 1.170)
	Il + Ac/Is/Pu	0.929*	(0.878, 1.020)	0.849**	(0.830, 0.948)	1.112	(1.039, 1.172)
	Il/Is+Pu/Ac	0.743**	(0.719, 0.867)	0.725**	(0.716, 0.873)	0.931**	(0.859, 1.058)
	Il + Pu/Is/Ac	0.781**	(0.763, 0.901)	0.838*	(0.809, 0.967)	0.950**	(0.876, 1.083)
	Il + Is/Pu/Ac	0.787**	(0.765, 0.927)	0.777**	(0.740, 0.937)	0.982**	(0.891, 1.108)
2 modules	Il + Is/Pu + Ac	0.907	(0.849, 1.008)	0.932	(0.862, 1.046)	1.095	(1.023, 1.133)
	Il + Pu/Is+Ac	0.883*	(0.814, 0.979)	0.897	(0.850, 1.004)	1.063	(0.991, 1.116)
	Il + Ac/Is+Pu	0.831*	(0.772, 0.940)	0.732**	(0.715, 0.886)	1.018	(0.946, 1.091)
	Il/Is+Pu + Ac	0.829*	(0.769, 0.930)	0.730**	(0.719, 0.871)	1.024	(0.954, 1.098)
	Is/Il + Pu + Ac	0.897	(0.820, 1.009)	0.932	(0.885, 1.029)	1.066	(0.992, 1.131)
	Pu/Il + Is+Ac	0.924	(0.868, 1.039)	0.861	(0.795, 0.993)	1.121	(1.030, 1.184)
	Ac/Il + Is+Pu	0.723**	(0.661, 0.902)	0.801*	(0.735, 0.979)	0.880**	(0.804, 1.047)

was more constrained in the evolution of carnivorans than jaw shape, because skull structure is a compromise between different functions (e.g., feeding, olfactory sense, vision, and brain processing) and is thus more difficult to modify than the mandible, only involved in food acquisition and processing. This suggests that the flexibility of the modular pattern in the carnivoran pelvic girdle could arise also from functional grounds. In any case, further studies will be necessary for testing this hypothesis.

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Compliance with Ethical Standards

Conflicts of Interest The authors declare that there are no conflicts of interest.

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