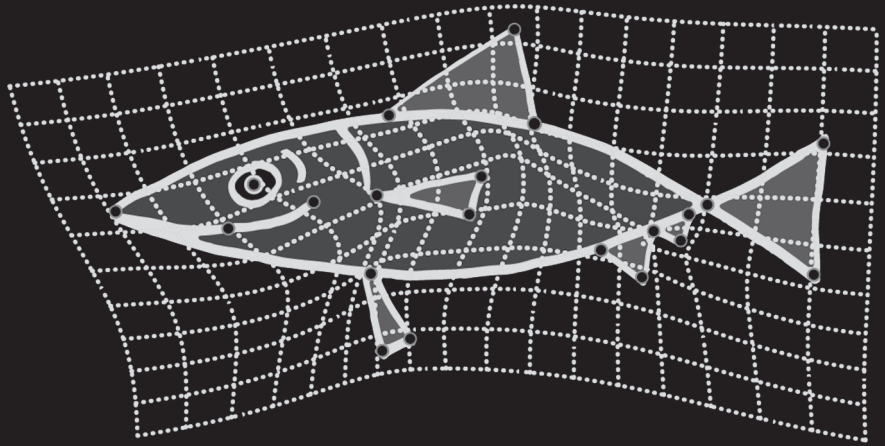


Conference proceedings

II IBERIAN SYMPOSIUM ON GEOMETRIC MORPHOMETRICS

Madrid, June 9th-10th, 2016



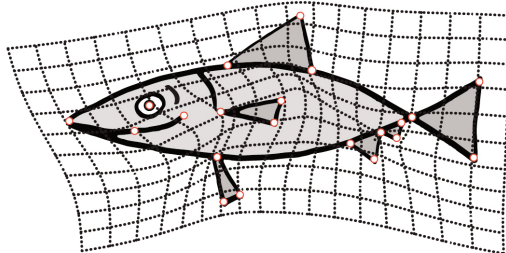
Institut Català de Paleontologia
Miquel Crusafont

PALEONTOLOGIA I EVOLUCIÓ, MEMÒRIA ESPECIAL 8

CONFERENCE PROCEEDINGS
OF THE
II IBERIAN SYMPOSIUM ON GEOMETRIC MORPHOMETRICS

Madrid, June 9th-10th, 2016

II ISGM



**II IBERIAN SYMPOSIUM ON
GEOMETRIC MORPHOMETRICS**

EDITORS

Carlos Martínez-Pérez

Judit Marigó

Soledad De Esteban-Trivigno

M^a Dolores Marin-Monfort

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Madrid, June 9th-10th, 2016

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PROGRAMME

WEDNESDAY June 8th

- 18:00 - 20:00 Registration
 20:00 - 21:30 Ice-Breaker

THURSDAY June 9th

- 9:00 - 11:30 Registration

9:00 - 9:30 Opening**Invited talk**

- 9:30 - 10:30 "OUTLINE ANALYSIS", THE CINDERELLA OF GEOMETRIC MORPHOMETRICS
 A. Baltanás

Oral Communications: Session 1 (Chairman: A. Baltanás)

- 10:30 - 10:50 SHAPE DIVERSITY OF OTOLITHS OF DIFFERENT FISH FAMILIES
 C. Llopis-Belenguier, A.E. Ahuir-Baraja, J.A. Balbuena, A. Rodríguez-González
- 10:50 - 11:10 MORPHOMETRIC TOOLS TO IDENTIFY TWO SYMPATRIC LIMPETS (*PATELLA RUSTICA* AND *PATELLA CAERULEA*) IN THE WESTERN MEDITERRANEAN
 P. Marti-Puig, M. Ponti, P.G. Albano, F. Costantini, M. Abbiati
- 11:10 - 11:30 MORPHOLOGICAL CHANGES OF INVASIVE TADPOLES CONFRONTED WITH NATIVE COMPETITORS ALONG THE INVASION RANGE
 E. Pujol-Buxó, A. Kaliontzopoulou, G.A. Llorente

11:30 - 12:00 Coffee Break**Oral Communications: Session 2 (Chairwoman: A. Kaliontzopoulou)**

- 12:00 - 12:20 A GEOMETRIC MORPHOMETRICS METHOD FOR EXPLORING DORSAL HEAD SHAPE IN URODELES: SEXUAL DIMORPHISM AND GEOGRAPHIC VARIATION IN *SALAMANDRA SALAMANDRA*
 L. Alarcon-Rios, G. Velo-Antón, A. Kaliontzopoulou
- 12:20 - 12:40 HABITAT RELATED DIFFERENCES IN HEAD SHAPE AND BITE PERFORMANCE IN THE GENERALISTIC LIZARD *PODARCIS BOCAGEI*
 V. Gomes, M.A. Carretero, A. Kaliontzopoulou
- 12:40 - 13:00 COMBINING GEOMETRIC MORPHOMETRICS WITH FINITE ELEMENTS ANALYSIS IN ARMADILLOS
 S. De Esteban-Trivigno, J. Marcé-Nogué, J. Fortuny, J. Cantalapiedra
- 13:00 - 13:20 GEOMETRIC MORPHOMETRICS AND THE MORPHOLOGICAL EVOLUTION OF THE EARLY DEVONIAN CONODONT *POLYGNATHUS*: FUNCTIONAL IMPLICATIONS
 C. Martínez-Pérez, G. Navalón, S. De Esteban-Trivigno, H. Botella

13:20 - 13:40 GEOMETRIC MORPHOMETRIC ANALYSIS ON LIVING SHARK CAUDAL FINN FOR ECOMORPHOLOGICAL INFERENCES FOR EARLY VERTEBRATES
H.G. Ferrón, H. Salais-López, C. Martínez-Pérez, H. Botella

13:40 - 15:00 Lunch

Oral Communications: Session 3 (Chairman: B. Figueirido)

15:00 - 15:20 MORPHO-FUNCTIONAL PATTERNS OF THE AVIAN FEEDING APPARATUS
G. Navalón, J. Marugán-Lobón, J.A. Bright, E.J. Rayfield

15:20 - 15:40 FUNCTIONAL ASSOCIATIONS BETWEEN SUBSTRATE USE AND FORELIMB SHAPE IN STREPSIRRHINES AND ITS RELEVANCE TO INFERRING LOCOMOTOR BEHAVIOR IN EARLY PRIMATES
A.-C. Fabre, J. Marigó, M.C. Granatosky, D. Schmitt

15:40 - 16:00 RECONSTRUCTING THE LOCOMOTOR BEHAVIOUR OF HOMINOIDS THROUGH THE BONY LABYRINTH: THE CONTRIBUTION OF 3D GEOMETRIC MORPHOMETRICS
A. Le Maître, P. Vignaud, M. Brunet

16:00 - 16:30 Coffee Break

Oral Communications: Session 4 (Chairwoman: C. Rissech)

16:30 - 16:50 A GEOMETRIC MORPHOMETRIC RECONSTRUCTION OF THORAX FORM IN *HOMO NALEDI*
M. Bastir, D. Garcia Martínez, M. Oishi, N. Ogiyara, I. Torres Sanchez, F. García Río, S. Nalla, P. Schmid, S. Churchill, J. Hawks, L. Berger, S.A. Williams

16:50 - 17:10 3D GEOMETRIC MORPHOMETRICS OF THE COLD-ADAPTED THORAX: ECO-GEOGRAPHICAL VARIABILITY OF THE HUMAN RIB CAGE
D. García-Martínez, S. Nalla, R.A. Guichón, M.D. D'Angelo, S. Constantino, F. García-Río, I. Torres, M. Bastir

Poster Session

17:10 - 18:00 RIGID ROTATION OF THREE-DIMENSIONAL STRUCTURES: STANDARDISED SPINNING PROCEDURE FOR COMBINED SHAPE ANALYSES OF ARTICULATED 3D STRUCTURES WITH APPLICATION FOR GEOMETRIC MORPHOMETRICS
M. Vidal-García, L. Bandara, J.S. Keogh

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Z. Chikhaoui, F. Krouchi, M. Lateb, A. Derridj

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S.J. van de Kerke, C. Broek, L. Schat, E. Schranz, F.T. Bakker

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IS THE ASTRAGALUS A GOOD BONE FOR INFERRING LOCOMOTION IN EXTINCT PRIMATES?

J. Marigó, A.-C. Fabre, D.M. Boyer

OUTLINE ANALYSIS OF THE GENERA *CRICETODON* AND *HISPANOMYS* AND ITS USE AS A TAXONOMICAL CRITERIA

P.M. Carro-Rodríguez, P. López-Guerrero, M.Á. Álvarez-Sierra

INFLUENCE OF TAXONOMIC AND ECOLOGICAL FACTORS ON THE CRANIAL MORPHOLOGY OF PRIMATES

M. Martín-Caballero, L. Medialdea, A. González

CRANIAL VARIABILITY IN EUROPEAN POPULATIONS OF BOTTLENOSE DOLPHIN *TURSIOPS TRUNCATUS* (CETACEA, ODONTOCETI, DELPHINIDAE): IMPLICATIONS FOR CONSERVATION

M.C. de Francesco, D. Kerem, A. Loy

DENTAL MORPHOMETRIC EVOLUTION IN RECENT SPANISH POPULATIONS

S. Torrijo-Boix, A. Romero

MORPHOLOGICAL VARIATION AND INTEGRATION OF DENTITION IN RED-FOX-LIKE (*VULPES*) AND SOUTH AMERICAN FOX-LIKE (*CERDOCYON*, *PSEUDOALOPEX*) CANIDS

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GEOMETRIC MORPHOMETRICS APPLIED TO ORNITHOPOD TRACKS FROM THE LOWER CRETACEOUS (BERRIASIAN) OF THE IBERIAN RANGE

D. Castanera, J.I. Canudo

COMPREHENSIVE MORPHOMETRIC ANALYSIS OF WILD AND FARMED GILTHEAD SEABREAM (*SPARUS AURATA*, L. 1758) IN THE EASTERN ADRIATIC SEA

I. Talijančić, T. Šegvić-Bubić, L. Grubišić, I. Katavić, I. Žužul

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J. Ventura, J. Martínez-Vargas, F. Muñoz-Muñoz

CHANGING MODULAR PATTERNS IN THE EVOLUTION OF THE CARNIVORE PELVIC GIRDLE

A. Martín-Serra

LIMB CO-VARIATION AND FLUCTUATING ASYMMETRY IN THE *MUS MUSCULUS* HYBRID ZONE

N. Skrabar, L.M. Turner, B. Harr, L.F. Pallares, D. Tautz

ASSESSING SKULL ASYMMETRIES IN AN ANCIENT IBERIAN ELIPOMETRICAL HORSE POPULATION

P.M. Parés-Casanova, N. Carolino, I. Carolino, J.V. Leite, R. Dantas, S. Lopes, J. Pèrez Paz, J. González Troncoso

APPLICATION OF GEOMETRIC MORPHOMETRICS TO SYMMETRY ASSESSMENT OF DIATOM FRUSTULES AS AN INDICATOR OF HEAVY METAL CONTAMINATION

D.C. Cubillos-A., J.T. Delgado-P., R.G. Barragán-G

COMPARATIVE MORPHOMETRIC ANALYSIS OF POSTERIOR PALATAL DEVELOPMENT
DISRUPTED BY FGFR MUTATIONS IN CRANIOSYNOSTOSIS SYNDROMES

F. Melkonian, S.M. Perrine, E.W. Jabs, J.T. Richtsmeier, N. Martínez-Abadías

Invited talk

18:00 - 19:00 ALLOMETRIC SPACES AND GEOMETRIC MORPHOMETRICS: AN APPROACH FOR
STUDYING THE EVOLUTION OF ALLOMETRY
C.P. Klingenberg

FRIDAY June 10th

Oral Communications: Session 5 (Chairman: C.P. Klingenberg)

9:30 - 9:50 ONTOGENY OF THE FEMUR AND FEMORAL DIMORPHISM IN A SPANISH
POPULATION BASED ON TELEMETRIES AND GEOMETRIC MORPHOMETRICS
C. Rissech, A. Pujol, J. Ventura, D. Turbón

9:50 - 10:10 SEXUAL DIMORPHISM IN MODERN HUMAN SKULL DURING ONTOGENY
L. Medialdea, A. Romero, A. González

10:10 - 10:30 GEOMETRIC MORPHOMETRIC EVALUATION OF PROXIMAL HUMERUS METAPHYSIS
AND ITS RELATIONSHIP TO SKELETAL MATURATION
R. García-González, A. Salazar, Y. Quintino, L. Rodríguez, J.M. Carretero

10:30 - 10:50 HETEROCHRONY IN NOTOSUCHIA (CROCODYLIFORMES, MESOEUCROCODYLIA):
ARE BAURUSUCHIDS PERAMORPHIC?
P.L. Godoy, G.S. Ferreira, B.C. Vila Nova, F.C. Montefeltro, M.C. Langer

10:50 - 11:10 COMPARISON OF MANDIBLE FORM BETWEEN WILD AND LABORATORY MICE
DURING EARLY POSTNATAL ONTOGENY.
J. Martínez-Vargas, F. Muñoz-Muñoz, A. Molinero, M.J. López-Fuster, J. Ventura

11:10 - 11:30 ALLOMETRY, INTEGRATION, MODULARITY AND THE EVOLUTION OF PHENOTYPIC
DIVERSITY IN A GROUP OF LIZARDS WITH HIGH MORPHOLOGICAL VARIATION
A. Kaliontzopoulou

11:30 - 12:00 **Coffee Break**

Oral Communications: Session 6 (Chairwoman: N. Martínez-Abadías)

12:00 - 12:20 MODULARITY OR INTEGRATION OR BOTH? 3D ANALYSIS OF 21 GENERA OF FROGS
DEMONSTRATES PHYLOGENETIC CONSERVATISM IN SKULLS AND LABILITY IN LIMBS
M. Vidal-García, J.S. Keogh

12:20 - 12:40 EVOLUTIONARY MODULARITY AND MORPHOLOGICAL INTEGRATION IN THE
HAPTORAL ANCHORS STRUCTURES OF THE *LIGOPHORUS* SPP. (MONOGENEA,
DACTYLOGYRIDAE)
A. Rodríguez-González, R. Míguez-Lozano, V. Sarabeev, J.A. Balbuena

12:40 - 13:00 THE ROLE OF DEVELOPMENT AND ARTIFICIAL SELECTION ON ELBOW-JOINT
PHENOTYPIC DISPARITY IN DOMESTIC DOGS
B. Figueirido

13:00 - 13:20 EVOLUTIONARY DEVELOPMENT OF THE CARNASSIAL TOOTH IN EXTANT CANIDS USING GEOMETRIC MORPHOMETRICS
P.A. Márquez-González, J. Muñoz-Durán

13:20 - 13:40 GEOMETRIC MORPHOMETRICS AS A TOOL FOR CHARACTERIZING DOG DIVERSITY IN IBERIAN LATE PREHISTORY
A. Daza, A. Morales, C. Liesau, C. Azorit

13:40 - 15:00 Lunch

Oral Communications: Session 7 (Chairman: D. Rasskin-Gutman)

15:00 - 15:20 STUDY OF THE ACETABULUM OF PRIMATES USING GEOMETRIC MORPHOMETRICS
M. San Millán, A. Kaliontzopoulou, C. Rissech, D. Turbón

15:20 - 15:40 RELIABILITY OF ESTIMATING PHYLOGENIES FROM SHAPE AND SIMILAR MULTIDIMENSIONAL DATA
C. Varón-González, S. Whelan, C.P. Klingenberg

15:40 - 16:00 ADDING PHYLOGENETIC TREES TO IMPROVE VIRTUAL RETRODEFORMATION: CERCOPITHECIDAE AS A TEST CASE
M. Tallman, N. Amenta, E. Delson, S.R. Frost, D. Ghosh, F.J. Rohlf

16:00 - 16:20 GEOMETRIC MORPHOMETRICS AND REFERENCE SYSTEMS IN COMPARATIVE ANATOMY
J. Marugán

16:20 - 17:00 Coffee Break

Oral Communications: Session 8 (Chairman: B. Hallgrímsson)

17:00 - 17:20 SYNOSTOSIS AND VERTEBRATE SKULL EVOLUTION: FROM BONE NETWORKS TO BONE SHAPE
D. Rasskin-Gutman, J.M. Sanchís García, B. Esteve-Altava, A. Navarro Díaz, I. Rasskin, R. Diogo

17:20 - 17:40 HOW MORPHOMETRICS CAN SHED LIGHT INTO GENETICS, DEVELOPMENT AND DISEASE
N. Martínez-Abadías, R. Mateu, J. Sastre, L. Russo, J. Richtsmeier, J. Sharpe

17:40 - 18:00 FACIAL PHENOTYPE IN DOWN SYNDROME CHILDREN: EXPLORING THE EFFECTS OF EPIGALLOCATECHIN-3-GALLATE
R. González, J. Starbuck, J. Sharpe, R. de la Torre, M. Dierssen, N. Martínez-Abadías

Invited talk

18:00 - 19:00 INTEGRATION, NONLINEARITIES AND THE LOGIC OF DEVELOPMENT.
B. Hallgrímsson

19:00-19:30 Closure

21:00 Closure Dinner

A GEOMETRIC MORPHOMETRICS METHOD FOR EXPLORING DORSAL HEAD SHAPE IN URODELES: SEXUAL DIMORPHISM AND GEOGRAPHIC VARIATION IN *SALAMANDRA SALAMANDRA*

L. Alarcon-Rios^{1,2*}, G. Velo-Antón³, A. Kaliontzopoulou³

1 Departamento de Biología de Organismos y Sistemas, Ecology Area, Universidad de Oviedo, Oviedo, Spain.

2 Unidad Mixta de Investigación en Biodiversidad (UMIB), CSIC-Universidad de Oviedo-Principado de Asturias, Mieres, Spain.

3 CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Instituto de Ciências Agrárias de Vairão, Universidade do Porto, Vairão, Portugal.

*Corresponding author e-mail address: alarconlucia@uniovi.es

The study of morphological differences among and within taxa can shed light on the evolutionary forces acting on species. In the case of urodeles, the dorso-ventral view of the head captures most of the ontogenetic and evolutionary variation of the entire head, which is a structure with a high potential for being a target of selection due to its relevance in several ecological and social functions. Here, we describe a non-invasive protocol for using geometric morphometrics for exploring morphological variation in the external dorso-ventral view of urodeles' head. To test the accuracy of the method we applied it to two NW Iberian populations of *Salamandra salamandra gallaica*. Despite the high intraspecific diversity within *S. salamandra*, neither sexual dimorphism in shape nor morphological variation among populations have been explored in depth. This method detected differences in head shape among populations, among sexes and an allometric relationship between shape and size, although no differences in allometric trends were detected among groups. It also allowed us to determine that not all differences in head shape are due to differences in size, indicating differential growth across sexes and populations. The method present

ed here allowed to detect shape variation at a very fine scale, and solves the drawbacks of using cranial samples, thus increasing the possibilities of using collection specimens and alive animals for exploring dorsal head shape variation and its evolutionary and ecological implications in urodeles.

“OUTLINE ANALYSIS”, THE CINDERELLA OF GEOMETRIC MORPHOMETRICS

Á. Baltanás^{1*}

¹ Dept. Ecology / Faculty of Sciences, Universidad Autónoma de Madrid, Spain.

*Corresponding author e-mail address: angel.baltanas@uam.es

Landmark-based methods are considered to be “the norm” in Geometric Morphometrics; a well-earned statement given that these methods are firmly supported by statistical shape theory. Unfortunately, not all interesting biological objects have enough landmarks (sometimes they have no true Type-I landmarks at all) to make morphometric analysis using landmark-based methods feasible. In such cases, the shape can be captured by the coordinates of a sequence of points along the outline of the object, a function can be fitted to such sequence of points, and the function parameters —assumed to be descriptors of shape— can be then submitted to multivariate analysis. That is what “Outline Analysis” is all about.

This approach, “Outline Analysis”, has a long history that predates the advent of landmark-based methods; includes a handful of techniques (from different types of Fourier descriptors to eigenshape analysis and Bezier curves); has been applied to many different kinds of biological (and non-biological) objects; is available in many software packages; and, like any other methodology, displays strengths and weaknesses. But despite its remarkable contribution to the study of biological form and its potential as a complement to land-

mark-based methods, it has been frequently undervalued and even ignored. Accordingly, the aim of this contribution is to bring to the audience an updated summary of the history, methods, applications and achievements of “Outline Analysis” in order to —like happened to Cinderella, the folk tale character— attain recognition or success after a period of oblivion and neglect.

A GEOMETRIC MORPHOMETRIC RECONSTRUCTION OF THORAX FORM IN *HOMO NALEDI*

M. Bastir^{1,2*}, D. Garcia Martínez^{1,2}, M. Oishi³, N. Ogiwara⁴, I. Torres Sanchez⁵, F. García Río⁵, S. Nalla^{2,6}, P. Schmid², S. Churchill^{2,7}, J. Hawks^{2,8}, L. Berger², S.A. Williams^{2,9}

1 Paleoanthropology Group, Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain.

2 Evolutionary Studies Institute and Centre for Excellence in PalaeoSciences, University of the Witwatersrand, South Africa.

3 Department of Veterinary Anatomy, School of Veterinary Medicine, Nippon Veterinary and Life Science University, Tokyo, Japan.

4 Department of Mechanical Engineering, Faculty of Science and Technology, Keio University, Yokohama 223-8522, Japan.

5 Hospital Universitario La Paz, Biomedical Research institute (Idipaz), Madrid, Spain.

6 Department of Human Anatomy and Physiology, Faculty of Health Sciences, University of Johannesburg, PO Box 524, Auckland Park, 2006, South Africa.

7 Department of Evolutionary Anthropology, Box 90383, Duke University, Durham, NC 27708, USA.

8 Department of Anthropology, University of Wisconsin-Madison, Madison, WI 53593, USA.

9 Center for the Study of Human Origins, Department of Anthropology, New York University, 25 Waverly Place, New York, NY 10003, USA.

*Corresponding author e-mail address: mbastir@mncn.csic.es

Homo naledi shows a mosaic morphological pattern with modern features in the skull, wrists, thumbs and feet and primitive features in the metacarpals, the shoulder girdle, ribs and pelvis. This morphology reflects a hominin at the transition between *Australopithecus* and *Homo*. Two thoracic vertebrae (T10, T11) and ribs (11th, 12th) were found in anatomical connection, belonging thus to the same individual. Here we explore these anatomically connected lower thorax fossils to develop a quantitative 3D ribcage reconstruction of *H. naledi*. We measured 526 3D-(semi)landmarks on human and hominoid ribcages for geometric morphometric analyses (N=33). We analyzed thorax variation by principal components analysis and covariation between the shapes of isolated 11th thorax segment and the full remaining ribcage by partial least squares analyses. Results suggest that the ribcage of *H. naledi* is caudally wider than cranially. This reflects a primitive, funnel-shaped thorax. However, the strong declination of the ribs in the costo-vertebral joint does not fully fit with such a pattern and requires more research. The thorax of *H. naledi* is thus more similar to non-human primates and *Australopithecus* than modern humans. This hypothesis is also supported by a wide, flared upper pel-

vis, which altogether suggests a primitive trunk (and body) shape. Functionally, such a body shape is suboptimal for effective bipedalism and contrasts with the fully modern anatomy of the foot skeleton of *H. naledi*. On the other hand, a narrow upper thorax and shoulder girdle allows for increased upper limb mobility that, together with its primitive curved metacarpals, is beneficial for arboreal locomotion. The evidence suggests therefore a hominin capable to cover wide ranges of locomotion in arboreal and terrestrial habitats. Better preserved trunk remains are necessary to clarify the functional and evolutionary morphology of this newly discovered hominin fossils.

OUTLINE ANALYSIS OF THE GENERA *CRICETODON* AND *HISPANOMYS* AND ITS USE AS A TAXONOMICAL CRITERIA

P.M. Carro-Rodríguez^{1*}, P. López-Guerrero^{1,2}, M.Á. Álvarez-Sierra^{1,2}

1 Departamento de Paleontología, Universidad Complutense de Madrid, C/ José Antonio Novais 12, 28040 Madrid, Spain.

2 Departamento de Geología Sedimentaria y Cambio Medioambiental, Instituto de Geociencias IGEO (CSIC, UCM), C/ José Antonio Novais 12, 28040 Madrid, Spain.

*Corresponding author e-mail address: patcarro@ucm.es

Cricetodon and *Hispanomys* (Rodentia, Mammalia) include several species that illustrate the mosaic evolution. Therefore, the generic assignation of some of these species is controversial. Agustí (1982) remarked that *Ruscinomys* and some species of *Hispanomys* present trilobed contour, whereas *Cricetodon* has it straight. Also, López-Guerrero *et al.* (2015) suggest the contour of the anterior upper molars (M1) as a discriminatory generic character. The contour can be studied by using the Fourier method. We applied Fourier method on the photographs of 56 M1s belonging to *Cricetodon meini* from Vieux-Collonges (middle Aragonian, middle Miocene) and *Hispanomys aragonensis* from Pedregueras 2A, 2C, 1C and Nombrevilla 14 (early Vallesian, late Miocene). These species were used as a case study because there is no doubt in their generic assignation and they present very different contours: straight—*Cricetodon*— and trilobed—*Hispanomys*—. Our aim is to study whether the differences that are observed in the M1 contour between these two species could be statistically tested. Using Fourier methodology, we have performed a Principal Component, a cluster and a discriminant analyses. The results show differences between the two species. The PCA reveals

two distinct groups that correspond to the two species. Furthermore, the cluster analysis also reveals two large, distinct groups. Finally, the discriminant analysis supports the results above with a significant p-value<0.001. This work reveals that Fourier analysis can differentiate two types of contour: trilobed and straight. Our work will provide new criteria that could help to determinate the generic assignation of species like “*Cricetodon*” *fandli* or “*Cricetodon*” *klariankae*.

Agustí, J. (1982). Tendencias evolutivas de la línea *Cricetodon-Ruscinomys* (Rodentia, Mammalia) en la Península Ibérica. *Acta Geologica Hispanica* 17, 103-111.

López-Guerrero, P., García-Paredes, I., Prieto, J., López-An-toñanzas, R., Álvarez-Sierra, M.A. (2015). Paleodiversity of *Cricetodontini* during the late Aragonian (middle Miocene) from the European basins. *Palaeobiodiversity and Palaeoenvironments* 95, 415-430.

GEOMETRIC MORPHOMETRICS APPLIED TO ORNITHOPOD TRACKS FROM THE LOWER CRETACEOUS (BERRIASIAN) OF THE IBERIAN RANGE

D. Castanera^{1*}, J.I. Canudo²

1 Bayerische Staatssammlung für Paläontologie und Geologie and GeoBioCenter, Ludwig-Maximilians-Universität, Richard-Wagner-Str. 10, 80333 Munich, Germany.

2 Grupo Aragosaurus-IUCA, Facultad de Ciencias, Universidad de Zaragoza, Pedro Cerbuna 12, E-50009 Zaragoza, Spain.

*Corresponding author e-mail address: d.castanera@lrz.uni-muenchen.de

Shape analysis has previously been used to generate a morphospace for dinosaur tridactyl footprints (Rasskin-Gutman *et al.*, 1997). By applying geometric morphometrics (GM), different theropod ichnotaxa were analysed using principal component analysis (PCA) and thin-plate spline methods (Castanera *et al.*, 2015). Following the same procedure, six specimens of the unnamed ornithopod tracks from Las Cerradicas tracksite (Berriasian, Villar del Arzobispo Formation, Teruel province) and 17 specimens of the ichnotaxon *Iguanodontipus? oncalensis* (Berriasian, Huérteles Formation, Soria province) have been analysed. Our aim is to determine if there is a considerable shape variation between these two types of footprints or not, and thus to try to clarify the ichnotaxonomic relationships of the former tracks. The first two components represent 62.79% of the morphological variation. The PCA shows two clear convex hulls although these are very close in the morphospace and the 95% confidence ellipses partially overlap. According to the loadings data, the shape deformation graph and thin-plate splines, the main differences lie on the landmarks that represent the location of the "heel" and the most distal position of digits II and IV. These landmarks are thus related

to differences in the digit length and the divarication angles between digits II-IV, suggesting that the unnamed ornithopod tracks from Las Cerradicas are slightly more elongated. Further work is needed in order to establish whether these differences are sufficient to classify these tracks as different ichnotaxa or not.

Castanera, D., Colmenar, J., Sauqué, V., Canudo, J.I. (2015). Geometric morphometric analysis applied to theropod tracks from the Lower Cretaceous (Berriasian) of Spain. *Palaeontology* 58(1), 183-200.

Rasskin-Gutman, D., Hunt, G., Chapman, R.E., Sanz, J.L., Moratalla, J.J. (1997). The shapes of tridactyl dinosaur footprints: procedures, problems and potentials. In: D.L.Wolberg, E. Stump, G.D. Rosenberg (eds.), *Dinofest International proceedings. Academy of Natural Sciences, Philadelphia*: 377-383.

VARIABILITY OF LEAF SHAPE ALONG THE SHOOT IN *ACER MONSPESSULANUM* AS REVEALED BY GEOMETRIC MORPHOMETRICS

Z. Chikhaoui^{1*}, F. Krouchi¹, M. Lateb¹, A. Derridj¹

1 Faculté des Sciences Biologiques et des Sciences Agronomiques, Université Mouloud MAMMERI, BP 17, Tizi-Ouzou, Algérie.

*Corresponding author e-mail address: c_zakia@hotmail.fr

Geometric Morphometric analysis (i.e. Landmark method) was undertaken in 346 leaves of the Montpellier Maple (*Acer monspessulanum* L.) in order to study their within-tree morphological variability.

Sampling was done in 30 different trees located in the Djurdjura Mountain (Algeria) during autumn 2014. In each tree, 3 new shoots were harvested around canopy. Within each shoot, leaves were considered with respect of their insertion (i.e. basal, median and apical leaves). Then, leaves were pressed, dried and scanned with the abaxial face uppermost. The data analysis method used was that of Viscosi & Cardini (2011). Eleven landmarks

were digitized on each leaf using TpsDig2. The obtained data was analyzed using Anova and PCA in MorphoJ.

Results showed a marked change in leaf conformation along the shoot. As a consequence, such within-tree variation should be taken into account in future systematic investigations aiming at discriminating between species and their putative hybrids in the Djurdjura.

Viscosi, V., Cardini, A. (2011). Leaf Morphology, Taxonomy and Geometric Morphometrics: A Simplified Protocol for Beginners. PLoS one 6(10), e25630.

APPLICATION OF GEOMETRIC MORPHOMETRICS TO SYMMETRY ASSESSMENT OF DIATOM FRUSTULES AS AN INDICATOR OF HEAVY METAL CONTAMINATION

D. C. Cubillos-A.¹, J. T. Delgado-P.¹, R. G. Barragán-G.^{1*}

1 Ingeniería Ambiental. Universidad Santo Tomás, Carrera 9 No. 51-11. Bogotá D.C., Colombia.

*Corresponding author e-mail address: rafaelbarragan@usantotomas.edu.co

This project aimed to generate an economic and reliable detection tool to be potentially implemented in continuous water quality monitoring protocols by means of the analysis of morphological changes presented in the frustules of diatoms as a heavy metal contamination.

A laboratory experiment and a sampling field campaign along the upper Bogotá river basin (Cundinamarca, Colombia) were performed. The experiment consisted of 8 different morphotypes incubated together in confined wetland water enriched with hexavalent chromium (CrVI) under 10, 50 and 100 mg/l CrVI concentration for ten days. Each treatment was evaluated for morphology deviations every three days. The other source of diatoms was the epilithic community that thrived at each of the four transects where pooled samples were taken and fixed with ethanol. Once at the laboratory, aliquots of both sources were digested with H₂O₂, HCl and NH₃, before dehydration over a glass slide for the subsequent observation and image capture through the 40X or 100X microscope magnifiers with a coupled digital camera and image administration software. The image processing and data analysis were performed with the R project software by adapting some digitalization

steps (evaluation of landmarks quantity for deformities detection, landmarks order according to symmetry) and database structure to fulfill the geomorph package requirements (splitting of data sets, lists formatting). The analysis consisted in the exploration of three ways for data interpretation for the detection of morphology deviations: i) anova, ii) PCA and iii) allometric analysis. From the statistical analyses there was generated enough statistical evidence for morphotypes differentiation for both the experiment and the samples from the river. Although the digitalization steps will have to be improved; also, were detected the effect of altitudinal gradient along the basin over the morphometric variables, and the particular sensibility to CrVI contamination of one morphotype.

GEOMETRIC MORPHOMETRICS AS A TOOL FOR CHARACTERIZING DOG DIVERSITY IN IBERIAN LATE PREHISTORY

A. Daza^{1*}, A. Morales², C. Liesau^{1,2}, C. Azorit³

1 Departamento de Prehistoria y Arqueología. Universidad Autónoma de Madrid. Avenida Tomás y Valiente, 1 Campus de Cantoblanco, 28049 Madrid, Spain.

2 Laboratorio de Arqueozoología, Universidad Autónoma de Madrid. C/ Darwin, 2, 28049 Madrid, Spain.

3 Departamento de Biología Animal, Biología Vegetal y Ecología. Facultad de Ciencias Experimentales y de la Salud (B3), 23071, Jaén, Spain.

*Corresponding author e-mail address: arantzazu.daza@uam.es

This work addresses the phenomenon of dog differentiation in Iberian Late Prehistory (IIIrd and IInd millennia B.C.) through a Geometric Morphometrics (GM) analysis of dog mandibles. One major aim of the study was to ascertain whether the specific places where Chalcolithic and Bronze Age dog remains had been deposited evidenced any kind of correspondence with the morphology of this bone.

Traditional osteometric analyses carried out on these same dogs have thus far shown a high degree of homogeneity as well as an overall uniformity in terms of height at the withers. Furthermore the use of traditional indexes is limited by defective preservation as many of the limb bones used in these analyses were either fractured or eroded. In contrast, a previous GM study on the mandibles proved its usefulness to statistically discriminate among groups of apparently very similar morphology. This presentation enlarges our previous database, originally centered on the Chalcolithic Period, with adding new specimens from this period and from the Bronze Age and elaborates on the discriminant power of GM to allocate mandibles from prehistoric dogs in manners that touch upon issues dealing with the ecology, evolution and domestication of dogs in Iberia.

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COMBINING GEOMETRIC MORPHOMETRICS WITH FINITE ELEMENTS ANALYSIS IN ARMADILLOS

S. De Esteban-Trivigno^{1,2*}, J. Marcé-Nogués³, J. Fortuny^{1,4}, J. Cantalapedra⁵

1 Institut Català de Paleontologia M. C., Edifici Z, c/de les Columnes s/n, Campus de la UAB. E-08193 Cerdanyola del Vallès, Spain.

2 Transmitting Science, Gardenia 2, Piera, 08784, Barcelona, Spain.

3 Universität Hamburg Centrum für Naturkunde, Martin-Luther-King-Platz 320146 Hamburg, Germany.

4 Centre de Recherches en Paléobiodiversité et Paléoenvironnements, Muséum national d'Histoire naturelle, Bâtiment de Paléontologie, CP38, 8 rue Buffon, 75005 Paris, France.

5 Museum für Naturkunde, Leibniz-Institut für Evolutions & Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Invalidenstr. 43, D-10115, Berlin, Germany.

*Corresponding author e-mail address: soledad.esteban@transmittingscience.org

Xenarthra is an American clade that was widespread in the past whose diversity has been greatly reduced, being now represented only by sloths, anteaters and armadillos. Armadillos are the most diverse group of extant xenarthrans, with more than 30 species included in 3 subfamilies.

The objective of this work was to explore the co-variation between biomechanical performance, diet and the shape of the lower jaw of 11 species of extant armadillos.

We used Finite Element Analysis (FEA) to analyze the biomechanical performance of the lower jaw under equivalent loads. In order to combine stress data with shape data we developed novel procedures to generate quantitative variables of the stress data from FEA. On the other hand, geometric morphometrics was used to obtain shape variables for the lower jaw. 2D landmarks were digitalized on lateral pictures of mandibles belonging to different armadillo species.

After doing a Principal Components Analysis (PCA) the first PC (75 % variance) was mostly related to shape differences associated with diet (insectivorous vs omnivorous) with exception of one species, *Cabassous unicinctus*. Insectivorous armadillos have a slender mandible, with the ascending

ramus developing a wider angle with the dentary. Furthermore, PC2 (14.2 % of explained variance) described the main shape differences between Tolypeutinae and the rest of subfamilies, characterised by a reduced coronoid process, independently of their diet.

Shape variables have a phylogenetic signal, on the contrary, some of the biomechanical indicators show no phylogenetic signal. Both Partial Least Squares (PLS) and regressions support a strong relationship between the jaw shape and the levels of stress.

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CRANIAL VARIABILITY IN EUROPEAN POPULATIONS OF BOTTLENOSE DOLPHIN *TURSIOPS TRUNCATUS* (CETACEA, ODONTOCETI, DELPHINIDAE): IMPLICATIONS FOR CONSERVATION

M.C. de Francesco^{1*}, D. Kerem², A. Loy¹

1 Dep. Biosciences and Territory, University of Molise, Fonte Lappone, Pesche (IS) 86090, Italy.

2 Charney School of Marine Sciences, University of Haifa, Mt. Carmel, Haifa 31905, Israel.

*Corresponding author email address: maria.defrancesco@unimol.it

The recognition of distinct geographical populations and the identification of their local adaptive traits represent critical information for the prioritization of conservation efforts, especially in wide ranging species like dolphins. Following previous evidence of isolation of Mediterranean vs. Atlantic stocks in the striped and the common dolphins, we aimed at elucidating whether the same phenotypic pattern occurs in the bottlenose dolphins. Size and shape variation were evaluated through 2D GM of the skull and the mandible of 338 specimens. Landmark configurations of various projections were transformed through GPA (Rohlf & Slice, 1990), differences among populations examined through ANOVA and MANOVA of logCS shape variables. Results revealed the existence of six distinct populations: three in the Mediterranean Sea, two in the Atlantic Ocean, and one in the North/Baltic Sea, partly confirming previous observations (Natoli *et al.*, 2005; Sharir *et al.*, 2011). UPGMA derived from Mahalanobis distances revealed two main clusters, including respectively the Mediterranean and extra-Mediterranean samples thus confirming the pattern found in other dolphin species. Lateral and medial mandible projections host the most diagnostic traits, likely linked to adaptative feeding and

sound reception pressures. Significant size and allometric differences were also found among all populations.

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Sharir, Y., Kerem, D., Gol'din, P., Spanier, E. (2011). Small size in the common bottlenose dolphin *Tursiops truncatus* in the eastern Mediterranean: a possible case of Levantine nanism. *Marine Ecology Progress Series* 438, 241-251.

Rohlf, F.J., Slice, D. (1990). Extensions of the Procrustes Method for the Optimal Superimposition of Landmarks. *Systematic Zoology* 39(1), 40-59.

FUNCTIONAL ASSOCIATIONS BETWEEN SUBSTRATE USE AND FORELIMB SHAPE IN STREPSIRRHINES AND ITS RELEVANCE TO INFERRING LOCOMOTOR BEHAVIOR IN EARLY PRIMATES

A.-C. Fabre^{1,2*}, J. Marigó^{1,3,4}, M.C. Granatosky¹, D. Schmitt¹

1 Department of Evolutionary Anthropology, Duke University, Durham, NC 27708, USA.

2 UMR 7179 MECADEV - C.N.R.S., M.N.H.N, Département d'Ecologie et de Gestion de la Biodiversité, Muséum national d'Histoire naturelle, 75005 Paris, France.

3 UMR 7207 CR2P - C.N.R.S., M.N.H.N., U.P.M.C.-Paris 6. Département Histoire de la Terre, Muséum national d'Histoire naturelle, 75005 Paris, France.

4 Institut Català de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de Barcelona, Edifici Z (ICTA-ICP), Carrer de les Columnes s/n, Campus UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain.

*Corresponding author e-mail address: acfabre@mnhn.fr

The evolution of primates is intimately linked to their initial invasion of a complex arboreal environment with a wide variety of substrate inclinations and diameters. It is widely assumed that primate species are behaviorally and anatomically adapted to movement and foraging on specific substrates within the arboreal milieu, but few explicit tests of this relationship in an evolutionary context have been conducted. Without direct tests of form-function relationships in living primates it is impossible to reliably infer behavior in fossil taxa. In this study, we aim to test a hypothesis of co-variation between forelimb morphology and the type of substrates used by strepsirrhines in order to test for associations between anatomy and substrate use that can then be applied to limb anatomy of extinct primates. The co-variation between each forelimb long bone and the type of substrate used were studied in a phylogenetic context. Our results show that there is a strong phylogenetic signal for the shape of each long bone of the forelimb. However, clear support use associations are present as well. Co-variation was found between the type of substrate used and the shape of the radius, with and without taking into account the phylogeny, whereas the co-variation was only significant for

the ulna when taking into account the phylogeny. Species associated with the utilization of a thin branch milieu show radii that are gracile and straight and have a distal articular shape that allows for a wide range of movements. In contrast, extant species associated with large supports show a relatively robust and curved radius with increased surface area available for forearm and hand muscles in pronated posture. These results, especially for the radius, support the idea that many strepsirrhine primates exhibit specific skeletal adaptations associated with the supports that they habitually move on.

GEOMETRIC MORPHOMETRIC ANALYSIS ON LIVING SHARK CAUDAL FINN FOR ECOMORPHOLOGICAL INFERENCES IN EARLY VERTEBRATES

H.G. Ferrón^{1*}, H. Salais-López², C. Martínez-Pérez¹, H. Botella¹

1 Departamento de Geología, Universitat de València, C/ Dr Moliner, 50, Burjassot, València, 46100, Spain.

2 Departamento de Biología Funcional y Antropología Física, Universitat de València, C/ Dr Moliner 50, Burjassot, València, 46100, Spain.

*Corresponding author e-mail address: Humberto.Ferron@uv.es

Body design of aquatic vertebrates is closely related with swimming mode (Webb, 1975) and feeding strategies (Webb, 1984). Here, the morphological variability of lateral shape of extant sharks has been analysed in 438 species by means of geometric morphometric analysis using ten landmarks (type 1 and 2). PCA and regression analysis between shape and body length have been performed. PCA results were interpreted classifying sharks both into taxonomical groups and according to their mode of life. Our results suggest morphological convergence in non-close related shark species that share similar modes of life. We have also found a notable homogeneity in the caudal fin morphology of active pelagic sharks, most of them sharing the possession of a well-developed ventral lobe and high caudal fin span in proportion to the total body length, thus maximizing thrust and minimizing drag and recoil energy losses. Besides ecology, our results suggest that caudal fin morphology is also influenced by the body size. We have found interspecific positive allometry affecting mainly the caudal fin span of living sharks. This same phenomenon has been previously reported during the ontogeny of some phylogenetically distant aquatic vertebrates, including bony fishes, cetaceans and

even fossil groups such as ichthyosaurs (Motani, 2002), responding to common physiological constraints. In this way, it is established a useful comparative framework for inferring some anatomical aspects in extinct early vertebrates that not always are preserved in the fossil record (e. g. some osteostracans, placoderms, acanthodians and some chondrichthyans) from paleoecological data and vice versa.

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THE ROLE OF DEVELOPMENT AND ARTIFICIAL SELECTION ON ELBOW-JOINT PHENOTYPIC DISPARITY IN DOMESTIC DOGS

B. Figueirido^{1*}

1 Departamento de Ecología y Geología, Área de Paleontología, Facultad de Ciencias, Universidad de Málaga, 29071 Málaga, Spain.

*Corresponding author e-mail address: [Borja.figueirido@uma.es](mailto:borja.figueirido@uma.es)

The rapidly originated large-scale phenotypic diversity of domestic dogs (*Canis familiaris*) by artificial selection is often considered an adaptive radiation at intraspecific level. Accordingly, dogs provide a unique opportunity to study the range and limits of phenotypic diversity with very simple genetic variation and skeletal disparity. Here I quantify elbow joint phenotypic disparity in dogs to investigate the role of artificial selection and developmental constraints on forelimb bone design. I use landmark-based methods of geometric morphometrics in 2D to capture the shape of the elbow joint, as it is an established morphological indicator of forearm motion, and hence, of locomotor adaptations in mammalian carnivores. My main goal is to assess if a morpho-functional structure of limbs such as the elbow has been limited to evolve or, conversely, it has evolved by artificial selection.

A Principal Components Analysis revealed that elbow joint phenotypic disparity in dogs is not higher than the disparity observed in living canines, but it is significantly lower than in the extinct hesperocyonine and borophagine canid subfamilies, and in other families of carnivorans analyzed (i.e., Felidae, Hyaenidae). A canonical variates analysis indicates a possible absence of functional signal in

dog breeds, as there is not evidence of convergence for forearm motion between wild carnivores and dog breeds adapted for fast speeds (e.g., the cheetah [*Acinonyx jubatus*] vs. greyhounds) or for manipulation (e.g., pantherines to grapple with prey vs. fighting dogs). Our data preliminarily indicates that once the canine subfamily achieved a cursorial-like elbow, this has not been substantially modified as in wild carnivores towards fast-speeds, forearm manipulation, or any other function. Therefore, the elbow joint seems to be a morphological structure that has not been subject to artificial selection by breeders.

GEOMETRIC MORPHOMETRIC EVALUATION OF PROXIMAL HUMERUS METAPHYSIS AND ITS RELATIONSHIP TO SKELETAL MATURATION

R. García-González^{1*}, A. Salazar¹, Y. Quintino¹, L. Rodríguez¹, J.M. Carretero¹

¹ Laboratorio de Evolución Humana, Área de Paleontología, Dpto. de CC. Históricas y Geografía, Edificio I+D+i, Universidad de Burgos, 09001 Burgos, Spain.

*Corresponding author e-mail address: mrgarcia@ubu.es

Among the numerous published methods for estimating age in growing individuals, just some of them are based on skeletal maturity. Although the most used methods to assess skeletal maturity are those based on the knee and the wrist, shape changes in other skeletal regions have provided useful information on the developmental or skeletal age of one individual. However, little attention has been focused in the shoulder region, including the proximal humerus. As far as we know, only the study by Ogden *et al.* (1978) pointed out that while the humeral epiphysis retained the shape from birth to adulthood, the humeral proximal metaphysis gradually changes from a rounded to an angulated surface.

Usually, these types of studies are based on roentgenograms and the shape changes are mainly expressed by qualitative criteria. In this work we explore humeral proximal metaphysis shape by means of geometric morphometrics in an attempt to provide comprehensive quantitative measurements of shape changes during humeral maturation. The sample is composed of 30 dentally aged skeletons housed in the Laboratory of Human Evolution at the University of Burgos. Right humeri were scanned with the NextEngine's

Desktop 3D Scanner and treated with the software ScanStudio. In the virtual models, a total of 4 landmarks and 30 sliding semilandmarks were placed using the R package geomorph. Principal component analysis in shape and form spaces was used to evaluate shape patterns. Our preliminary results show that shape changes along the first five principal components depict ontogenetic shape changes in humeral metaphysis. Since dental age is the most precise surrogate of chronological age, maturity changes in humeral proximal metaphysis could be particularly useful for estimating the skeletal age of juvenile skeletons.

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3D GEOMETRIC MORPHOMETRICS OF THE COLD-ADAPTED THORAX: ECO-GEOGRAPHICAL VARIABILITY OF THE HUMAN RIB CAGE

D. García-Martínez^{1,2*}, S. Nalla^{2,3}, R.A. Guichón⁴, M.D. D'Angelo^{4,5}, S. Constantino⁶, F. García-Río⁷, I. Torres⁷, M. Bastir^{1,2}

1 Paleoanthropology Group, Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain.

2 Evolutionary Studies Institute and Centre for Excellence in Palaeosciences, University of the Witwatersrand, South Africa.

3 Department of Human Anatomy and Physiology, Faculty of Health Sciences, University of Johannesburg, South Africa.

4 Laboratorio de Ecología Evolutiva Humana (LEEH), Núcleo de Estudios Interdisciplinarios de Poblaciones Humanas de Patagonia Austral (NEIPHA), Facultad de Ciencias Sociales (FACSO), Universidad del Centro de la Provincia de Buenos Aires (UNCPBA), CONICET, Argentina.

5 Laboratorio de Poblaciones de Pasado (LAPP), Departamento de Biología, Facultad de Ciencias, Universidad Autónoma de Madrid (UAM), C/Darwin 2, E-28049, Madrid, España.

6 Cátedra de Diagnóstico por Imágenes en Facultad de Medicina FASTA, Instituto Radiológico Mar del Plata, Argentina.

7 Hospital Universitario La Paz, Biomedical Research Institute (IdiPAZ), Madrid, Spain.

*Corresponding author e-mail address: dan.garcia@mncn.csic.es

Despite the importance of the thorax for human biology, its 3D morphological variability associated to eco-geographical variation is poorly understood. Allen's and Bergmann's eco-geographic rules link body size and shape to climate conditions in homoeothermic mammals. The majority of the authors claim that these rules also apply for humans adapted to extreme climate conditions (cold/warm). Thus, circumpolar people would present broader trunks and thoraces than people inhabiting mid-latitudes. However, other authors defend that these rules do not apply for humans because of technological adaptations (e.g. clothing and shelter). The present work address whether there are differences in costal morphology between populations inhabiting different climatic conditions. We quantified 3D-morphology of individual ribs (2-10) from populations inhabiting different climatic conditions (moderate—Europeans=216; warm - Sub-Saharan=126; cold - Greenland Inuits=98 and Tierra del Fuego=54) through 3D geometric morphometrics of landmarks and sliding semilandmarks (N=61). GPA and PCA was performed to reduce dimensionality of the data and explore variability. PC1-PC2 projection shows morphological variability linked to position, from

upper (short tubercle-angle distance; pronounced axial curvature; no torsion) to lower ribs (large tubercle-angle distance; less axial curvature; torsion). Upper ribs (2-4) from Tierra del Fuego present greater axial curvature than their counterparts of other populations, whereas rib 10 from Inuit and Tierra del Fuego present less. PC3 is linked to differences in axial curvature not related to position, where Inuit ribs are different from rest of the sample by less axial curvature and shorter rib shaft height. Our results show morphological differences in costal sequence of Inuit and Tierra del Fuego, which is probably due to morpho-functional adaptations of the thorax to cold climates. However, since they do not share a common morphological pattern, this could be produced by different degrees of coldness.

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HETEROCHRONY IN NOTOSUCHIA (CROCODYLIFORMES, MESOEUCROCODYLIA): ARE BAURUSUCHIDS PERAMORPHIC?

P.L. Godoy^{1*}, G.S. Ferreira², B.C. Vila Nova², F.C. Montefeltro³, M.C. Langer²

1 School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, B15 2TT, Birmingham, United Kingdom.

2 Laboratório de Paleontologia de Ribeirão Preto, FFCLRP, Universidade de São Paulo, Av. Bandeirantes 3900, 1404901, Ribeirão Preto, SP, Brazil.

3 Departamento de Biologia e Zootecnia, FEIS, Universidade Estadual Paulista (UNESP), Rua Monção 226, 15385-000, Ilha Solteira, Brazil.

*Corresponding author e-mail address: pedrolorenagodoy@gmail.com

Notosuchia is the most diverse clade of Gondwanan crocodyliforms, and its taxonomic and ecological diversity is demonstrated by the great morphological disparity exhibited by its members. Among the many groups within Notosuchia, Baurusuchidae stands out due to its peculiar cranial morphology, compatible with the role of the clade as top predators in Cretaceous ecosystems. However, despite the large number of species (at least 10) and specimens described, ontogenetic studies on baurusuchids are scarce, mostly because the juvenile specimens described are fragmentary. We present a complete skull of a juvenile specimen of *Pissarrachampsa sera* (Baurusuchidae), which sheds light on ontogeny within Notosuchia and the modifications that led to the highly modified skull of mature baurusuchids. To test if these modifications are already present in juvenile baurusuchids we performed a 2D geometric morphometrics analysis (in MorphoJ), including 24 notosuchian taxa (*Pissarrachampsa* represented by juvenile and adult individuals), and carried out Principal Component (PCA), Canonical Variate (CVA), and Discriminant Function analyses, in lateral and dorsal views of the skull. In the PCA morphospace of the first two

PCs (responsible for 64.5% and 62.6% of the variation in lateral and dorsal views, respectively), the juvenile *Pissarrachampsa* clusters with *Sphagesauridae*, a group of peculiar omnivorous/herbivorous notosuchians, and is closer to other putative omnivorous taxa, such as *Notosuchus* and *Marillasuchus*, than to adult baurusuchids. This indicates, at least considering the skull variation represented by these two PCs, a morphological resemblance between the juvenile *Pissarrachampsa* and forms with more generalist feeding behaviors. The consistent position of *Notosuchus*, *Marillasuchus*, and *Sphagesauridae* as immediate outgroups to Baurusuchidae allow us to use those species as proxies to infer the ancestral condition. Accordingly, their close proximity to the juvenile *Pissarrachampsa* in the morphospace suggests that the specialized mature baurusuchid skull represents a peramorphic modification of the plesiomorphic morphology of the group.

HABITAT RELATED DIFFERENCES IN HEAD SHAPE AND BITE PERFORMANCE IN THE GENERALISTIC LIZARD *PODARCIS BOCAGEI*

V. Gomes^{1,2*}, M.A. Carretero¹, A. Kaliontzopoulou¹

1 CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas N° 7, 4485-661 Vairão, Vila do Conde, Portugal.

2 Departamento de Biologia da Faculdade de Ciências da Universidade do Porto, Porto, Portugal.

*Corresponding author e-mail address: veronica.a.s.g@gmail.com

In lizards, it has been demonstrated that morphological variation is tightly related with habitat use, and locomotion has been described as the principal mediator of this relationship. However, different habitats may also encompass different types of prey or different refuge use. In this study, we investigated intraspecific ecomorphological variation in the generalistic lacertid *Podarcis bocagei* by examining populations exploiting two different habitats: agricultural walls vs. sand dunes. In the laboratory, we quantified bite force, and took high-resolution photographs of the lateral view of the head, previously shown to be relevant for bite performance in these lizards. To capture variation in head shape, we digitized 12 lateral landmarks. After a Generalized Procrustes Analysis, to standardize size, location and orientation, we performed a Procrustes ANOVA to examine whether male and female lizards inhabiting the two habitat types differed in head shape. To better visualize shape variation in both sexes we described and compared shape change trajectories using phenotypic trajectory analysis. Finally, we investigated the association between head shape and bite force using two-block partial least squares. Our results showed that head shape was significantly different between

habitats and sexes. We found that individuals from walls had relatively elongated snout as compared to those from dunes. In addition, shape dimorphism trajectories differed significantly between habitats, indicating a change in the direction of sexual dimorphism. A significant association existed between head shape and bite force. This association also translated into differences in biting performance across habitats, where lizards from dunes bite harder than those from walls. Further studies investigating the relationship between prey availability and refuge use should be performed to confirm the ecological significance of the observed patterns.

FACIAL PHENOTYPE IN DOWN SYNDROME CHILDREN: EXPLORING THE EFFECTS OF EPIGALLOCATECHIN-3-GALLATE

R. González^{1,2}, J. Starbuck³, J. Sharpe^{1,2,4}, R. de la Torre⁵, M. Dierssen^{1,2}, N. Martínez-Abadías^{1,2,6*}

1 Center for Genomic Regulation (CRG), The Barcelona Institute of Science and Technology, Dr. Aiguader 88, 08003 Barcelona, Spain.

2 Universitat Pompeu Fabra (UPF), Barcelona, Spain.

3 University of Central Florida, 4000 Central Florida Blvd, Orlando, FL 32816-1361, USA.

4 Institució Catalana de Recerca i Estudis Avançats (ICREA), Pg. Lluís Companys 23, 08010 Barcelona, Spain.

5 Integrative Pharmacology and Systems Neuroscience, IMIM-Hospital del Mar Medical Research Institute, Barcelona, Spain.

6 Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Av. Diagonal 645, 08028 Barcelona, Spain.

*Corresponding author e-mail address: neus.martinez@crg.eu

Down syndrome (DS) is a genetic condition resulting from trisomy of chromosome 21 characterized by cognitive impairment, immunodeficiency, congenital heart diseases, skeletal and facial dysmorphologies. DS phenotypes are associated with the overexpression of genes located in the Down Syndrome Critical Region, such as *DYRK1A*. This gene encodes a protein kinase whose downstream targets are involved in neurogenesis and skeletal development. Epigallocatechin-3-gallate (EGCG), a green tea flavonoid, is a specific *DYRK1A* inhibitor that can normalize the expression of *DYRK1A* and improve cognitive deficits in both humans with DS and trisomic Ts65Dn mice. EGCG treatment can also rescue abnormal skeletal phenotype in DS mice, including the long bones and the craniofacial complex. Since *DYRK1A* is expressed within the facial prominences during embryonic development, we hypothesize that *DYRK1A* overexpression in craniofacial primordia may contribute to facial dysmorphology in DS. To test the effects of EGCG treatment in humans, we have performed a preliminary facial shape analysis comparing the faces of children from 1 to 18 years old distributed in 3 groups: 1) DS children 2) Euploid children 3) DS children treated with EGCG. Three-

dimensional photogrammetric images that accurately capture facial surface topography were acquired using a multi-camera system (3dMD). To characterize facial shape, we recorded 3D coordinates from 21 anatomical landmarks, and performed a General Procrustes analysis. Results of a principal component analysis (PCA) based on the Procrustes coordinates adjusted for size and age showed that the DS children are differentiated from the euploid children, whereas children with DS treated with EGCG tend to present an attenuated DS facial phenotype closer to the euploid average shape configuration. Further analyses with increased sample sizes and extended facial shape coverage using semilandmarks will be performed to assess whether a reduction in *Dyrk1a* overexpression via EGCG treatment can modulate the facial phenotype in DS.

INTEGRATION, NONLINEARITIES AND THE LOGIC OF DEVELOPMENTB. Hallgrímsson^{1*}

1 Department of Cell Biology & Anatomy, University of Calgary. HRIC 3A29, 3330 Hospital Drive NW, Calgary, AB T2N 4N1, Canada.

***Corresponding author e-mail address: bhallgri@ucalgary.ca**

Evolutionary developmental biology hinges on our ability to understand genotype-phenotype maps. For morphology, such maps are extraordinarily complex. Following Pere Alberch, I argue that a key goal is to search for regularities among the processes and mechanisms that link genetic to phenotypic variation. The study of developmental

integration reveals such regularities that can contribute significantly to our understanding of the relationship between genotype and phenotype. This middle-out approach is an important strategy in our quest to understand the genetics, development and evolvability of complex morphology.

ALLOMETRY, INTEGRATION, MODULARITY AND THE EVOLUTION OF PHENOTYPIC DIVERSITY IN A GROUP OF LIZARDS WITH HIGH MORPHOLOGICAL VARIATION

A. Kaliontzopoulou^{1*}

1 CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, Nº 7. 4485-661 Vairão, Vila do Conde, Portugal.

*Corresponding author e-mail address: antigoni@cibio.up.pt

Understanding the mechanisms that underlie the emergence and maintenance of phenotypic diversity is a main objective of evolutionary biology. Size-shape allometry, integration, and modularity reflect the major developmental mechanisms, such as canalization and plasticity, which determine phenotypic variation and constrain trait co-variation and responses to selective pressures. Wall lizards of the genus *Podarcis* exhibit high levels of morphological diversity and are an emerging model in evolutionary studies that investigate sources of phenotypic variation. The use of geometric morphometrics (GM) to study morphological patterns in relation to e.g. ontogeny, sexual dimorphism and habitat in this group indicates that head shape variation is usually manifested in an anterior-posterior direction, regardless of the focal biological factor. This finding suggests that head shape may be constrained in this group of lizards and makes them an interesting model to investigate how different mechanisms contribute to phenotypic diversity. I used GM to quantify dorsal and lateral head shape in a total of 876 individuals, representing 14 evolutionary lineages of Iberian and North African *Podarcis* by digitizing 24 dorsal and 12 lateral landmarks. After Procrustes superimposition, I exami-

ned size-shape allometry, I tested whether the head is structured in frontal-distal modular partitions, and investigated patterns of integration and their variation across lineages. The results obtained suggest that the lizard head is divided in an anterior and a posterior module with internal cohesiveness in terms of shape variance, both dorsally and laterally. These two modules are highly integrated with each other across the whole sample and within each lineage separately. Size-shape allometry enhances the degree of integration, which nevertheless remains significant once allometric effects are accounted for. However, allometric and integration patterns vary extensively across lineages, suggesting an important role of these mechanisms in determining the remarkable levels of phenotypic diversity observed in these lizards.

ALLOMETRIC SPACES AND GEOMETRIC MORPHOMETRICS: AN APPROACH FOR STUDYING THE EVOLUTION OF ALLOMETRY

C.P. Klingenberg^{1*}

1 Faculty of Life Sciences, University of Manchester, Michael Smith Building, Oxford Road, Manchester M13 9PT, United Kingdom.

*Corresponding author e-mail address: cpk@manchester.ac.uk

Comparisons of allometries have been performed for more than a quarter-century by multivariate ordinations using principal component analyses of the vectors of allometric coefficients. More recently, this approach has been named “allometric spaces”. So far, this approach has been used mostly in the context of traditional morphometrics, but not with geometric morphometrics. This pre-

sentation summarises recent developments that make it possible to use allometric spaces with geometric morphometric analyses of landmark data. The details of the methods depend on whether the analysis is based on a shape, form or conformation space. I will provide examples to illustrate these methods.

RECONSTRUCTING THE LOCOMOTOR BEHAVIOUR OF HOMINOIDS THROUGH THE BONY LABYRINTH: THE CONTRIBUTION OF 3D GEOMETRIC MORPHOMETRICS

A. Le Maître^{1*}, P. Vignaud¹, M. Brunet^{1,2}

1 Institut de Paléoprimateologie et Paléontologie Humaine : Evolution et Paléoenvironnements (IPHEP), UMR CNRS 7262 INEE, Université de Poitiers, Bât. B35 – TSA 51106, 6 rue Michel Brunet, 86073 Poitiers, France.

2 Chaire de Paléontologie humaine, Collège de France, 11 place Marcelin Berthelot, 75005 Paris, France.

*Corresponding author e-mail address: anne.le.maitre@univ-poitiers.fr; anne.le.maitre@ens-lyon.org

The labyrinth, or inner ear, is fundamental for posture and balance. Relationships exist between the morphology of the bony labyrinth and some locomotor behaviours such the human bipedalism or the relative agility. In mammals, these links were established based on linear and angular measurements. But studies conducted on other vertebrates show that geometric morphometrics can also be used.

In this study, we explore the potential of geometric morphometrics to link locomotion to the labyrinthine morphology in hominoids. The aim is to describe the locomotor behaviour more subtly than the broad locomotor classes already obtained with traditional morphometrics.

The sample comprises 65 specimens from five extant hominoid species: *Homo sapiens*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus* and *Hylobates lar*. The left bony labyrinth of each individual is virtually extracted and 22 landmarks are positioned. After a Procrustes superposition, a principal component analysis is conducted on the landmark spatial coordinates.

The morphological differences between the five species are statistically significant. The whole labyrinth, and more specifically the lateral semicir-

cular canal, is involved. The shape changes are diverse: orientation variations, rotations, projections and torsions.

Relative to the traditional morphometrics, the 3D geometric morphometrics add information on locomotion: each “specialist” species with a preferential locomotor mode is discriminated from the “generalist” semi-terrestrial species. This interesting result could be used to reconstruct the locomotor behaviour of fossil species, based on comparisons with extant species.

SHAPE DIVERSITY OF OTOLITHS OF DIFFERENT FISH FAMILIES

C. Llopis-Belenguer^{1,2*}, A.E. Ahuir-Baraja², J.A. Balbuena¹, A. Rodríguez-González¹

1 Marine Zoology Unit, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Valencia, Spain.

2 Research department, Avanqua Oceanogràfic-Àgora S.L. Eduardo Primo Yúfera No. 1B E-46013, Valencia, Spain.

*Corresponding author e-mail address: cristina.llopis.belenguer@gmail.com

In teleosts, otoliths are depositions of aragonite and organic materials. Otoliths represent three paired structures located at both sides of the brain, and are formed in the inner-ear. Otoliths are related to equilibrium and auditory functions. The otolith structures are termed *lapillus*, *asteriscus* and *sagitta*. The *sagitta* is usually the largest, and is used in morphometric studies. Here, we investigate the morphology of the *sagitta* from different fish species and we test the phylogenetic signal using GM (geometric morphometric) techniques. The study of shape and size of *sagitta* otoliths was based on Cartesian coordinates of three landmarks and 60 semilandmarks. The data set consisted of *sagitta* otoliths from 63 individuals, from 21 species, and 12 families. Procrustes analysis and PCA (Principal Component Analysis) were used to extract comparable shape information between structures. The allometric relationship between size and shape was evaluated by means of multivariate regression. The presence of a phylogenetic signal was tested by mapping the variation in shape and size onto previously published phylogenies. Finally, differences among species from different habitats were studied, using CVA (Canonical Variate Analysis).

The first two PCs explained 82.39% of the total variance. The allometric relationship between size and shape was not significant ($p > 0.05$). A significant phylogenetic signal was found for shape ($p < 0.05$) and marginally significant for size ($p = 0.05$). The CVA revealed significant differences among some groups. Our results agree with previous works that predicted differences in otoliths of different species, and this may be related with different sensitivities to different sound frequencies. Our analysis showed conserved morphology of otoliths within phylogenetically related species. We also found different morphologies between groups from different habitats and that might reflect environmental adaptation that assures optimal auditory function for each habitat.

IS THE ASTRAGALUS A GOOD BONE FOR INFERRING LOCOMOTION IN EXTINCT PRIMATES?

J. Marigó^{1,2*}, A.-C. Fabre^{3*}, D.M. Boyer⁴

1 UMR 7207 CR2P – C.N.R.S., M.N.H.N., U.P.M.C.-Paris 6, Département Histoire de la Terre, Muséum national d'Histoire naturelle, Paris, France.

2 Institut Català de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de Barcelona, Edifici Z (ICTA-ICP), Carrer de les Columnes s/n, Campus UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain.

3 UMR 7179 C.N.R.S./M.N.H.N., 57 rue Cuvier, Case postale 55, 75231, Paris Cedex 5, France.

4 Department of Evolutionary Anthropology, Duke University, Durham, NC, USA.

*Corresponding authors e-mail addresses: judit.marigo@mnhn.fr, acfabre@mnhn.fr

The astragalus of extinct primates has traditionally been used to infer locomotor behavior in fossil forms, using features such as the orientation of the trochlear rims or the astragalar neck, as well as the height of the astragalar body. In this study we use 3D geometric morphometric techniques in order to assess the phylogenetic signal of this bone as well as evaluate the covariation that exists between the shape of the astragalus and the type of locomotion, specifically the proclivity for leaping, and substrate use orientation (vertical/horizontal) in extant strepsirrhines.

To do so, we used 3D surface reconstructions from Morphosource (<http://morphosource.org/>) and locomotion and substrate use data from Oxnard and collaborators. Geometric morphometric data were taken on 95 astragali belonging to all the extant strepsirrhine families. We calculated the phylogenetic signal of the astragalus using a multivariate K and we assessed the covariation between its shape and locomotion type as well as substrate use orientation using two-block partial least squares.

Our preliminary results show that astragalus shape, locomotion and the tendency to leap have a strong phylogenetic signal. Astragalar shape and

locomotion strongly covary within extant strepsirrhines. However, when taking phylogeny into account, the results are no longer significant. The same is true when examining the covariation between astragalar shape and proclivity for leaping. In addition, we found that there is no covariation whatsoever between substrate use and astragalar shape, irrespective of whether phylogeny is taken into account or not.

The astragalus is a bone that has a strong phylogenetic signal. Thus, closely related species tend to present more similar astragali than species with similar locomotor repertoires. This should be taken into account when making functional interpretations of this bone in extinct forms because different astragalar shapes could in fact be more informative regarding phylogeny rather than locomotion.

EVOLUTIONARY DEVELOPMENT OF THE CARNASSIAL TOOTH IN EXTANT CANIDS USING GEOMETRIC MORPHOMETRICS

P.A. Márquez-González^{1*}, J. Muñoz-Durán²

1 Fachbereich 2- Biologie, Universität Bremen. Bibliothekstrasse 1, 28359 Bremen, Germany.

2 Departamento de Biología, Universidad Nacional de Colombia, Carrera 45 # 26-85, Bogotá, Colombia.

*Corresponding author e-mail address: marquez.paola@gmail.com

In this study we analyzed the form of the lower carnassial tooth of 33 extant species of the subfamily Caninae (Canidae, Carnivora). For this purpose we explored the relationship between the carnassial shape and different dietary habits and taxonomic genera. We analyzed the complete carnassial outline using semilandmarks to describe the profile of different parts of the tooth. Our modularity hypothesis is that the carnassial tooth in Caninae is composed of two modules: the trigonid and the talonid, which are related to grinding and slicing. The modularity test supports that the anterior part of the trigonid is a module relatively independent of the rest of the carnassial. Using the combination of PCA (Principal Component Analysis), modularity test, and multivariate regression, we could correlate the shape of the carnassial tooth, the different dietary groups and taxonomic genera. The first four PCs explain 80% of the variation and show that individuals appeared grouped by genera as well as guilds. In the morphospace, the carnivorans are located between omnivores and hypercarnivorans in the center of the positive side of the PC1 and PC2. We could also observe a high proximity in shape space among South American genera and *Vulpes*. At the same time we

could observe that insectivory in Caninae is represented by different carnassial shapes that could have evolved independently. We conclude that alimentary habits have a strong correlation with the form of the carnassial tooth.

MORPHOMETRIC TOOLS TO IDENTIFY TWO SYMPATRIC LIMPETS (*PATELLA RUSTICA* AND *PATELLA CAERULEA*) IN THE WESTERN MEDITERRANEAN

P. Marti-Puig¹, M. Ponti¹, P. G. Albano², F. Costantini¹, M. Abbiati³

1 BiGeA & CIRSA, Università di Bologna, UO CoNISMa, Via S. Alberto 163, 48123 Ravenna, Italy.

2 Institut für Paläontologie, Universität Wien Geozentrum, UZA II, room 2B411, Althanstraße 14, A-1090 Vienna, Austria.

3 ISMAR, Consiglio Nazionale delle Ricerche - Istituto di Scienze Marine, Bologna, Italy.

*Corresponding authors e-mail addresses: patypuig@gmail.com

Many marine organisms show a high morphological variability, which often represents a result of the phenotypic plasticity towards different environmental conditions they are exposed, such as wave exposure, substrate type and habitat. This variability can lead to species misidentification using simple visual inspection, with serious implications for monitoring activities and application of conservation policies. In the present study, morphological variability of two common limpets, which are subject to collection for human consumption, *Patella rustica* and *P. caerulea*, was studied in the western Mediterranean Sea. Morphological variability was analysed using morphometric shape analysis by se-

veral shape descriptors (Circularity, solidity, height/area, height/maximum diameter...) and by Elliptic Fourier Descriptors (EFDs) outline method. The genetic marker COI was used to support the identification of the sampled individuals. Some morphological traits (i.e. mean circularity, ratio height/longest diameter and solidity) and shape descriptors resulted useful measures to discriminate between the two species and quantify the morphological variability within the species. This study highlights the potential of morphometric tools as a non-destructive identification method to identify close related species.

INFLUENCE OF TAXONOMIC AND ECOLOGICAL FACTORS ON THE CRANIAL MORPHOLOGY OF PRIMATES

M. Martín-Caballero^{1*}, L. Medialdea¹, A. González¹

¹ Laboratorio de Poblaciones Antiguas del Pasado, Departamento de Antropología, Universidad Autónoma de Madrid, C/Darwin 2, Ciudad Universitaria de Cantoblanco, 28049, Madrid, Spain.

*Corresponding author e-mail address: marta.martinc01@estudiante.uam.es

Primates are a widely studied group due to their evolutionary proximity to humans. Cranial morphology of primates provides great information of their ecology and locomotion. This study aims to analyze and quantify changes in skull shape of different kinds of primates in terms of these two characteristics by means of Geometric Morphometric (GM) techniques. A sample of 24 adult male skulls belonging to 11 different genera was analyzed. 2D radiographs of the skull were taken and scanned and sets of landmarks (40 in front view and 25 in lateral view) were identified (Adobe Photoshop) and recorded (tpsDIG64). Generalized Procrustes Analysis was performed to remove size. Shape variation was analyzed by Principal Component Analysis (PCA) and differences in shape due to ecological and locomotion factors were quantified using a Discriminant Function Analysis (MorphoJ). The results showed over a 66% variation accumulated in the first two PCs of individuals analyzed in both views, being variations due to locomotion along the PC1 in both cases and ecology along the PC2 in side view. The analysis of the skull in lateral view allowed correct classification of individuals by means of their ecology and locomotion (65%, 80% respectively, $p < 0.0001$) while front view only sho-

wed a good classification by means of locomotion (90%, $p < 0.0001$). In conclusion GM techniques constitute a useful tool to analyze and quantify the differences in the shape of primates in terms of their ecology and locomotion. Further studies should be developed with larger samples for this purpose.

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CHANGING MODULAR PATTERNS IN THE EVOLUTION OF THE CARNIVORE PELVIC GIRDLE

A. Martín-Serra^{1*}

¹ Departamento de Ecología y Geología, Área de Paleontología, Facultad de Ciencias, Universidad de Málaga, 29071 Málaga, Spain.

*Corresponding author e-mail address: almarse@uma.es

The pelvic girdle connects the hind limb to the axial skeleton, anchoring muscles that are crucial for terrestrial locomotion in quadrupedal mammals. From a developmental perspective, each hemi-pelvis is composed of three different bones: ilium, ischium and pubis. Here we explore the presence of phenotypic modules in the carnivore pelvis (Mammalia, Carnivora). We used 3D landmarks digitized in a wide sample of living carnivores. Landmarks were registered for the four basic developmental units: ilium, ischium, pubis and acetabulum (the latter is considered as a different unit due to its close interaction with the femoral head). Next, we tested different modularity hypotheses that consider all possible modules formed by the combination of these four developmental units. For each hypothesis, we tested the presence of modules by comparing the strength of their morphological covariation (RV coefficient) with a randomized distribution of modules. The hypotheses with more statistical support using allometry-free shape variation analysis included the four original units as modules. However, when performing allometry-free independent contrasts, all modules disappeared, emerging, instead, a pattern of weak integration in the whole pelvis. The most probable cause of this

result is that the modular pattern is not uniform among carnivores. To check this hypothesis, we further explored, independently, the modular pattern of three carnivore families (i.e., Felidae, Canidae and Ursidae). The results obtained confirmed our hypothesis: each family showed a different modular pattern, with the basic four modules in felids, whereas for canids and ursids, the ilium and pubis formed a single module that, in the case of ursids, also involved the ischium. In conclusion, this result suggests that the evolution of the carnivore pelvic girdle involved changes in the phenotypic modular pattern during the early diversification of the group.

HOW MORPHOMETRICS CAN SHED LIGHT INTO GENETICS, DEVELOPMENT AND DISEASE

N. Martínez-Abadías^{1,2,3*}, R. Mateu^{1,2}, J. Sastre^{1,2}, L. Russo^{1,2}, J. Richtsmeier⁴, J. Sharpe^{1,2,5}

1 Center for Genomic Regulation (CRG), The Barcelona Institute of Science and Technology, Dr. Aiguader 88, 08003 Barcelona, Spain.

2 Universitat Pompeu Fabra (UPF), Barcelona, Spain.

3 Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Av. Diagonal 645, 08028 Barcelona, Spain.

4 Department of Anthropology, Pennsylvania State University, 409 Carpenter Building, University Park, PA 16803, Pennsylvania, USA.

5 Institució Catalana de Recerca i Estudis Avançats (ICREA), Pg. Lluís Companys 23, 08010 Barcelona, Spain.

*Corresponding author e-mail address: neus.martinez@crg.eu

Gene expression patterns underlie phenotypic variation, from normal to diseased-altered variation. To understand how differences in gene expression are translated into differences in morphology it is crucial to quantify gene expression patterns within developing structures along an ontogenetic sequence. Here we show how combining molecular biology techniques, such as whole-mount *in situ* hybridization (WISH), with image analysis, we can extend the use of Geometric Morphometrics (GM) to the analysis of gene expression domains. To illustrate the potential of our approach in evolutionary and biomedical research we use the mouse limb. Our first example is based on the GM analysis of a large sample of 2D pictures of limb buds from C57Bl6 mouse embryos between E10-E12 days post fertilization WISH-labeled for *Hoxa11* and *Hoxa13*, two relevant genes for limb patterning. Our results revealed high, non-random and gene-specific variation undergoing canalization during limb development, suggesting that the systematic characterization of phenotypic and genetic shape variation can reveal features of development and mechanisms underlying evolutionary processes. In our second example, we extend our approach to the analysis of 3D shapes and focus on the

comparison of mice carrying a mutation that causes a rare congenital disorder in humans, Apert syndrome, and their unaffected littermates. We assessed whether the FGFR2 P253R mutation induces limb malformations that can be associated with changes in the expression pattern of *Dusp6*, a downstream gene of the FGF/FGFR signaling pathway. Our results based on 3D landmark-based data recorded on optical projection tomography images of E11.5 mouse embryos labeled for *Dusp6*, showed size and shape differences in the limbs of mutant mice, suggesting a mechanism through which altered FGF/FGFR signaling contributes to limb malformations early in development. Applied to different species, our method could track development and investigate how evolution has modified common developmental patterns to generate morphological diversity.

GEOMETRIC MORPHOMETRICS AND THE MORPHOLOGICAL EVOLUTION OF THE EARLY DEVONIAN CONODONT *POLYGNATHUS*: FUNCTIONAL IMPLICATIONS

C. Martínez-Pérez^{1,2*}, G. Navalón^{2,3}, S. De Esteban-Trivigno^{4,5}, H. Botella¹

1 Department of Geology, University of Valencia, C/Dr. Moliner 50, 46100 Burjassot, Spain.

2 School of Earth Sciences, Life Sciences Building, University of Bristol, Bristol BS8 1TQ, United Kingdom.

3 Unidad de Paleontología, Facultad de Ciencias, Universidad Autónoma de Madrid, Campus de Cantoblanco, Madrid, Spain.

4 Transmitting Science, Gardenia 2, Can Claramunt, 08784 Piera, Barcelona, Catalonia, Spain.

5 Institut Català de Paleontologia Miquel Crusafont (ICP), Universitat Autònoma de Barcelona, Edifici Z (ICTA-ICP), Carrer de les Columnes s/n, Campus UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain.

*Corresponding author e-mail address: Carlos.Martinez-Perez@uv.es

Despite conodont studies are mostly based on morphological characters, few studies have explored the shape variation in conodonts by means of Geometric Morphometrics.

Here we used a geometric morphometric analysis to study the morphological variability and evolutionary changes of a group of species of the early Devonian (Emsian) genus *Polygnathus*, the most diverse and widespread Devonian to Lower Carboniferous conodont genus.

We defined 6 landmarks and 16 semilandmarks on 214 P1 conodonts from 18 species of the genus *Polygnathus*, comprising its first 15 Myr of evolution. We used TPS series for digitizing, and Generalized Procrustes Superimposition (GPA) and MorphoJ to explore the variability at different levels. Allometry was investigated on a smaller subset where size information was available.

Allometry accounted for less than 15 % of the subset variability. That means that differences in size introduced certain degree of variability that was not controlled for in the total sample. PCA on all individuals showed high overlapping between specimens from different taxa (maybe an allometry effect). Yet, some species can be clearly differentiated in the first PC.

Our data have a clear phylogenetic signal, concordant with the fact that phylogeny in this group is drawn from morphological characters of the conodont elements. Mapping the phylogeny on the shape data reveals a clear evolutionary trend from older to younger species, consisting in the acquisition of proportionally wider platforms in younger species.

These results, supports the Martínez-Pérez *et al.*'s (2016) proposal that the development of platforms in *Polygnathus*, a recurrent morphology acquired independently by many other lineages, could be interpreted as an adaptive shift towards the biomechanical improvement of the food acquisition and process.

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COMPARISON OF MANDIBLE FORM BETWEEN WILD AND LABORATORY MICE DURING EARLY POSTNATAL ONTOGENY

J. Martínez-Vargas^{1*}, F. Muñoz-Muñoz¹, A. Molinero², M.J. López-Fuster³, J. Ventura¹

1 Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia, Facultat de Biociències, Universitat Autònoma de Barcelona, Avinguda de l'Eix Central, Edifici C, E-08193 Bellaterra (Cerdanyola del Vallès), Spain.

2 Departament de Biologia Cel·lular, de Fisiologia i d'Immunologia, Facultat de Biociències, Universitat Autònoma de Barcelona, Avinguda de l'Eix Central, Edifici C, E-08193 Bellaterra (Cerdanyola del Vallès), Spain.

3 Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals and Institut de Recerca de la Biodiversitat (IRBio), Facultat de Biologia, Universitat de Barcelona, Barcelona, Spain.

*Corresponding author e-mail address: jessmv88@gmail.com

The house mouse (*Mus musculus*) is one of the animal models most widely used in biological research. Studies conducted with this species preferentially use classical inbred mouse strains, originated from the hybridization of different *M. musculus* subspecies. The mandible of the house mouse is a complex morphological structure that has become a key model system in many fields of knowledge. However, few works have dealt with its morphological variation over early postnatal ontogeny. Our goal is to compare the morphological variation of the mouse mandible from the 2nd to the 8th postnatal week between the C57BL/6J laboratory strain (N=51) and wild specimens of *M. musculus domesticus* (N=36), the major contributor to the genome of the C57BL/6J and many other classical inbred mouse strains. A set of 18 two-dimensional landmarks digitized on the lingual side of both the right and left hemimandibles of all specimens was used to analyze mandible form variation with the geometric morphometric techniques implemented in MorphoJ. The analyses of variance showed that mandible shape significantly differed between laboratory and wild mice in each postnatal week, and that the mandibles of laboratory mice grew faster from the 4th postnatal week. The prin-

cipal component analysis revealed that the two groups of mice had similar patterns of shape changes over postnatal ontogeny, since mice of consecutive ages from both groups showed a staggered distribution along the first axis, which accounted for 41.59% of total variation. The second axis explained 18.11% of total variation, which corresponded to mandible shape differences between laboratory and wild mice. The ontogenetic differences in mandible form detected between both groups of mice could be due to their distinct genomic constitution. We conclude that particular attention should be paid when extrapolating the pattern of skeletal growth from laboratory to wild mice.

GEOMETRIC MORPHOMETRICS AND REFERENCE SYSTEMS IN COMPARATIVE ANATOMY

J. Marugán-Lobón^{1,2*}

1 Unidad de Paleontología, Facultad de Ciencias, Universidad Autónoma de Madrid, Campus de Cantoblanco, Madrid, Spain.

2 Dinosaur Institute, Natural History Museum of Los Angeles, California, USA.

*Corresponding author e-mail address: jesus.marugan@uam.es

A long standing challenge in comparative morphology has been to find a coordinate system that helps making anatomical descriptions consistent among taxa. In vertebrates, craniofacial morphology has been largely described using the Frankfort plane, but also using Broca's plane, Reid's baseline, or the lateral semicircular canal—one of the three canals of the labyrinth within the inner ear—as reference systems for skull orientation. The available data, however, do not support the assumption that the orientation any of these baselines is inter-specifically constant. Thus, using this references as fixed orientation baselines across taxa, and consequently rotating skulls in a magnitude equivalent to their orientation, may yield an inaccurate perception of craniofacial organization. One of the greatest achievements of Geometric Morphometrics was finding a consistent reference coordinate system to consistently superimpose homologous landmarks. Indeed, the consensus became the Mean for multiple and mathematically justified reasons. Here, using geometric morphometrics in an inter-specific sample of fossil and extant saurischian dinosaurs (including a classic case in modern birds), I will illustrate why and how classic anatomical baselines, such as the lateral semicircular ca-

nals, render important problems for interpretative and descriptive purposes in anatomy

SEXUAL DIMORPHISM IN MODERN HUMAN SKULLS DURING ONTOGENY

L. Medialdea^{1,2*}, A. Romero², A. González¹

1 Laboratorio de Antropología Poblaciones del Pasado, Departamento de Biología, Universidad Autónoma de Madrid. C/ Darwin, 2. Ciudad Universitaria de Cantoblanco. 28049 Madrid, Spain.

2 Departamento de Biotecnología, Universidad de Alicante. 99 E-03080 Alicante, Spain.

*Corresponding author e-mail address: laura.medialdea@predoc.uam.es

Human skull is a modular structure in which different parts are influenced by genetic and developmental factors. However, scarce information exists about sexual ontogenetic shape trajectories. Here, we analyzed the sexual dimorphism changes on developmental age by means of Geometric Morphometric (GM) techniques. Our study includes 310 Portuguese individuals of known sex (158 males and 152 females), ranging from infancy to adulthood (7-99 age range). A set of 31 homologous landmarks were recorded from 2D digital images of the skull in lateral view. Quadratic distances between landmarks were minimized by means of generalized Procrustes analysis (GPA) and shape was quantified by Principal Component Analysis (PCA) after Procrustes superimposition. We found significant changes in skull shape (PC1 12.9% and PC2 11.4% of total variance) and size (CS), suggesting that ontogenic scaling contributes to morphometric variations at population level. When individuals were compared by sex and age ranges (7-10, 11-18 and 19-99 years), significant skull shape differences (Procrustes ANOVA; $p < 0.0001$) indicated dissimilar growth shape patterns for both sexes. Modest but significant correlations with both skull CS and developmental age ($r = 0.2-0.4$; $p <$

0.01) contributed to distinct face and neurocranial modules. Further, discriminant functions of GPA-coordinates showed 83% of study subjects correctly classified by means of sex. Our ontogenetic findings using GM show that modern human skull changes dramatically during growth affecting sexual dimorphism plasticity.

COMPARATIVE MORPHOMETRIC ANALYSIS OF POSTERIOR PALATAL DEVELOPMENT DISRUPTED BY FGFR MUTATIONS IN CRANIOSYNOSTOSIS SYNDROMES

F. Melkonian¹, S.M. Perrine², E.W. Jabs³, J.T. Richtsmeier², N. Martínez-Abadías^{1,4,5*}

1 Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Av. Diagonal 645, 08028 Barcelona, Spain.

2 Department of Anthropology, Pennsylvania State University, 409 Carpenter Building, University Park, PA 16803, Pennsylvania, USA.

3 Icahn School of Medicine at Mount Sinai, New York (NY), USA.

4 Center for Genomic Regulation (CRG), The Barcelona Institute of Science and Technology, Dr. Aiguader 88, 08003 Barcelona, Spain.

5 Universitat Pompeu Fabra (UPF), Barcelona, Spain.

*Corresponding author e-mail address: neus.martinez@crg.eu

The FGF/FGFR pathway is involved in multiple intracellular signalling throughout embryonic development and is highly active during palatogenesis. Normal palate development involves three key processes: palatal shelf growth, elevation and fusion. Genetic mutations on two fibroblast growth receptors (FGFR2 and FGFR3) may disrupt any of these processes, resulting in non-syndromic cleft lip and palate, and palatal malformations in autosomal congenital disorders such as Apert, Crouzon and Muenke syndromes. In a previous study using comparative 3D shape analysis of landmark based data recorded on high resolution micro CT scans of mutant and non-mutant littermates of murine models of these craniosynostosis syndromes, we found that the posterior aspect of the palate is the most affected region at birth. Here we extend our morphometric analysis focusing only on the shape of the palatine bones at two different developmental stages (embryonic day 17.5 (E17.5) and day of birth (P0)). Analyses based on semi-landmarks collected along the curved medial edge of the right and left palatine bones further refined the quantitative comparison of palatal dysmorphologies in craniosynostosis syndromes. After Procrustes superimposition on sliding semilandmarks, we assessed

through Principal Component Analysis the differences between and within these craniosynostosis syndromes using murine models for Apert ($Fgfr2^{+/S252W}$ and $Fgfr2^{+/P253R}$), Crouzon ($Fgfr2^{+/C342Y}$) and Muenke ($Fgfr3^{+/P244R}$) syndromes. Our results highlight the differences in the severity and onset time of the palatal malformations associated with each craniosynostosis syndrome, with Apert syndrome causing the earliest and most extreme palatal deformations, and Muenke syndrome the mildest dysmorphologies. These results underlie the potential of Geometric Morphometrics to provide a morphological readout for the genetic and developmental mechanisms associated with disease.

PHOTOGRAMMETRY: A “LOW-COST” METHOD TO RECONSTRUCT THE THREE-DIMENSIONAL FORM OF SMALL MAMMALS

F. Muñoz-Muñoz^{1*}, M. Quinto-Sánchez², J. Martínez-Vargas¹, R. González-José²

1 Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia, Facultat de Biociències, Universitat Autònoma de Barcelona, Avinguda de l'Eix Central, Edifici C, E-08193 Bellaterra (Cerdanyola del Vallès), Spain.

2 Centro Nacional Patagónico, Consejo Nacional de Investigaciones Científicas y Técnicas, Puerto Madryn, Argentina.

*Corresponding author e-mail address: francesc.munozm@uab.cat

Over the last few years, the field of morphometrics has undergone a profound revolution. During this time, digital imaging technology has made great strides and 3D (three-dimensional) imaging technology has become increasingly available. Nonetheless, many studies of 3D structures still use 2D (two-dimensional) data, even when this may result in the loss of important information. This is particularly so in the study of small mammals, since devices with enough precision for the 3D digitisation of small objects are the most expensive. Thus, the development of low-cost methods aimed at recovering 3D shape from small mammals would be of great interest. Photogrammetry, which allows obtaining 3D data at lower cost than with other 3D techniques, has been widely used in disciplines like geomorphology or architecture. Recently, some studies have started to use photogrammetry to recreate 3D models of animal phenotypes but, to our knowledge, it has not been applied to the study of small mammals or other small vertebrates. In this context, the aim of this study was to test the suitability of photogrammetric techniques to obtain 3D landmarks from mouse skulls as a model system for small mammals. Shape and size of 3D models obtained with photogrammetric techniques were

consistent among replicates, even when different sets of photographs were used. The linear measurements obtained from the 3D models were highly correlated with measurements obtained with callipers on actual crania, and differences between both sets of measures were smaller than those among individuals in most of the tested measures. These results show for the first time that photogrammetry is a precise technique for 3D form analysis of small mammals. Photogrammetry also proved to be accurate for obtaining linear measurements between 3D landmarks. However, further studies are needed to demonstrate whether this technique is also accurate at recreating 3D shapes.

MORPHOLOGICAL VARIATION AND INTEGRATION OF DENTITION IN RED-FOX-LIKE (*VULPES*) AND SOUTH AMERICAN FOX-LIKE (*CERDOCYON*, *PSEUDOALOPEX*) CANIDS

O. Nanova^{1*}

1 Zoological Museum, Moscow State University, Bolshaya Nikitskaya 2, Moscow 125009, Russia.

*Corresponding author e-mail address: nanovaolgag@gmail.com

We examined inter-species variation in the shape of upper toothrows and in their morphological integration in the genus *Vulpes* and fox-like South American canids using a geometric morphometrics approach. South American canids are members of a monophyletic taxon which is sister to wolf-like canids (Bardeleben *et al.*, 2005). The basal to the red-fox-like canids Gray fox *Urocyon cinereoargenteus* was also included in the analysis. In total, 259 specimens of 12 species were employed. We found that toothrow shape overlapped significantly among the three phylogenetically remote analyzed lineages, and that the generalized fox-like shape is precisely repeated several times through Canidae evolution. The most distinct species was the Arctic fox *Vulpes lagopus* which is specialized to Arctic conditions. This species possesses a retracted and wide snout. Inter-species variation in the *Vulpes* genus (after exclusion of the highly specialized Arctic fox) is generally explained by size-shape allometry. The smallest species (Fennec fox, *Vulpes zerda*, and Rüppell's fox, *Vulpes rueppellii*) have an enlarged first molar M1 in comparison with the largest species (Red fox, *Vulpes vulpes*). Size allometry is not significant for inter-species variation of South American fox-like canids. The covariance matrices

for all studied species were nearly equidistant. The similarity of covariance structure was shown among three phylogenetically distant groups of Canidae with similar morphology.

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MORPHO-FUNCTIONAL PATTERNS OF THE AVIAN FEEDING APPARATUS

G. Navalón^{1,2*}, J. Marugán-Lobón^{1,3}, J.A. Bright^{2,4}, E.J. Rayfield²

1 Unidad de Paleontología, Facultad de Ciencias, Universidad Autónoma de Madrid, Campus de Cantoblanco, Madrid, España.

2 School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Road, Bristol, BS8 1RJ, United Kingdom.

3 Dinosaur Institute, Natural History Museum of Los Angeles, California, USA.

4 Department of Animal and Plant Sciences, Alfred Denny Building, University of Sheffield, Sheffield, United Kingdom.

***Corresponding author e-mail address: gn13871@bristol.ac.uk**

Beak shape is one of the classic examples of trophic adaptation that led to the discovery of natural selection and the origin of evolutionary theory. In spite of numerous qualitative studies evaluating the interplay between beak shape and trophic ecology, a quantitative phylogenetically-comprehensive study of beak ecomorphology is still lacking. Using geometric morphometrics, we digitized beak shape of 176 extant birds (96 families) in lateral view and statistically tested the association between beak morphology and trophic ecology. Additionally, we calculated the mechanical advantage (MA) of the main adductor muscles of the skull for each species. Surprisingly, we found that neither beak shape nor MA are good predictors of trophic ecology in birds. 80% of the studied species show low MA values within a narrow range, implying that in most birds the beak is employed as a fast gape/low force mechanism. Clades utilizing pre-swallowing mechanical processing of food items are best categorized by the interplay between shape and MA, showing two very morphofunctional solutions; cracking/biting herbivorous birds, particularly parrots, exhibit deep and curved beaks along with the highest values of MA (i.e. enhanced bite force/slow gape speed), exploring more than

the upper half of the total range of values. By contrast, two of the three main clades of raptorial birds exhibit deep curved beaks with relatively low MA values, while falcons show substantially higher values of MA. These differences are definitely surprising and highlight the diversity of predatorial feeding strategies in extant birds. The extreme multi-functional nature of the beak (enhanced by the diversity of kinetic patterns), meaning many non-trophic selective pressures were likely involved in its origin and subsequent evolution, together with the tight morphological integration of the whole avian skull are proposed as putative evolutionary factors impeding a finer match between trophic ecology, bill shape, and mechanical performance in birds.

ASSESSING SKULL ASYMMETRIES IN AN ANCIENT IBERIAN ELIPOMETRICAL HORSE POPULATION

P.M. Parés-Casanova^{1*}, N. Carolino², I. Carolino², J.V. Leite³, R. Dantas³, S. Lopes³, J. Pèrez Paz⁴,
J. González Troncoso⁴

1 Department of Animal Production, University of Lleida, Catalonia, Spain.

2 Unidade de Recursos Genéticos, Reprodução e Melhoramento Animal, INRB, Vale de Santarém, Portugal.

3 Associação de Criadores de Equinos de Raça Garrana (ACERG), Vieira do Minho, Portugal.

4 Asociación Pura Raza Cabalo Galego, Tui, Galicia, Spain.

*Corresponding author e-mail address: peremiquelp@prodan.udl.cat

Ancient breed horses are particularly known for their ability to survive in harsh environments, and developmental instability could represent important mechanisms for their adaptation to them. In this study, skull symmetry variability of an ancient Iberian elipometrical horse population (*Garrano* and *Galego*) was investigated by means of a 2-D landmark-based method. For this purpose, we studied 31 skulls belonging to *Garrano* (n=27) and *Galego* (n=4) specimens on deposit at ACERG in Vieira do Minho (Portugal) and *Asociación Pura Raza Cabalo Galego* in Tui, Galicia (Spain) respectively. Although *Garrano* and *Galego* horses are two officially different recognized breeds, their phenotypic identity as well as a continuous genetic flow between them (they graze all year round freely on mountains) allow to consider both as a same population, and one can suspect no genetic bottlenecks as a result of consanguinity. The gender partition was not possible in most of specimens, so this variable was not considered. A total of 15 homologous landmarks were used to represent the shape of skull (ventral aspect). Individual images were landmarked in duplicates to detect errors in plotting. Data processing was done using TPS series and MorphoJ v. 1.06c. The analysis was done spe-

cifically for object symmetry, symmetry axis passing through the median plane (defined by 5 landmarks). Procrustes ANOVA showed that the asymmetry variations were due to FA ($p < 0.001$). Significant right-left shape variation was present ($p < 0.001$). With our data it is not possible to confirm the presence of DA ($p = 0.325$), and further analysis is required. If we consider FA as an indicator of individual quality of fitness, it could be explained by extreme environmental conditions and so subject to a high stress level.

MORPHOLOGICAL CHANGES OF INVASIVE TADPOLES CONFRONTED WITH NATIVE COMPETITORS ALONG THE INVASION RANGE

E. Pujol-Buxó^{1,2*}, A. Kaliontzopoulou³, G.A. Llorente^{1,2}

1 Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Barcelona, Spain.

2 Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Spain.

3 CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, University of Porto, Campus Agrario de Vairão, Vairão, Portugal.

*Corresponding author e-mail address: eudaldp@hotmail.com

The introduction, establishment and expansion of an invasive species creates a series of previously non-existent competitive interactions. If native competitors are not extinguished, these novel interactions can lead to fast evolutionary changes, both in the native and the invasive species. This means that biological invasions embody a good case for studying the evolution of characters related to interspecific competition, including phenotypic plasticity. Anuran tadpoles respond morphologically to a wide array of stimuli such as desiccation risk, predation risk, pollutants and competition pressure, and plastic changes have effects on immediate fitness and even mid- and long-term effects after metamorphosis. Here, we examine the morphological changes induced in tadpoles of an invasive anuran (*Discoglossus pictus*) linked to different combinations of high and low levels of desiccation risk and competitive pressure from a native species (*Bufo calamita*). To test possible changes in the competitive interactions among these species along the invasion range, we studied two populations with different evolutionary histories: one very near to the first introduction of the invasive frog (meaning approx. 100 years of coexistence with the native competitor) and another from the expansion

front of the species (less than 3 years of coexistence). As the native competitor is present all along the invasion range of the invasive frog, we hypothesized that outcomes should be more favorable to the invasive species in short-coexisting populations from the expansion front, where the native competitor is naive and the invasive species is not. Interestingly, most of our results (e.g. tadpole size, developmental rates and stability) support this idea. In addition, we found different allometric patterns and morphological plasticity among populations and experimental treatments, making this an interesting system to investigate how local adaptation and competition following an invasion determine morphological responses of native and invasive species.

SYNOSTOSIS AND VERTEBRATE SKULL EVOLUTION: FROM BONE NETWORKS TO BONE SHAPE

D. Rasskin-Gutman^{1*}, J.M. Sanchís García², B. Esteve-Altava³, A. Navarro Díaz¹, I. Rasskin⁴, R. Diogo⁵

1 Theoretical Biology Research Group. Institute Cavanilles of Biodiversity and Evolutionary Biology. University of Valencia, Valencia, Spain.

2 Pediatric Radiology. Clinical Hospital. University of Valencia, Valencia, Spain.

3 Structure & Motion Lab, Department of Comparative Biomedical Sciences, The Royal Veterinary College, Hatfield, United Kingdom.

4 Faculty of Mathematics. University of Montpellier, Montpellier, France.

5 Department of Anatomy, College of Medicine, Howard University, Washington DC, USA.

*Corresponding author e-mail address: diego.rasskin@uv.es

With the emergence of tetrapods, the skeleton has evolved in different directions, often accompanied by changes in size, locomotion, or dietary demand. Convergences are not unusual in the shape of anatomical structures, and the skull is not an exception. Sometimes it is possible to trace big macroevolutionary trends over long periods of time; the Willinston's Law is one such big trend, which documents the reduction of bone number in the skull. All major tetrapod lineages exhibit this pattern driven by two morphogenetic processes: bone loss and fusion, which also occur normally during development; however, when either of these processes happens at the wrong time, they may cause pathologies. For example, if closure timing is altered, it may cause well-known morphological changes in humans for both synostotic and non-synostotic bones. Using Anatomical Network Analysis (AnNA) we have studied these phenomena by considering bones as elements of connected networks that change when nodes or links disappear. Since the medical literature offers extensive evidence of the relationship between fusion of bones and shape changes, the question that arises naturally is: can a model of shape change based on bone fusion provide a basis for the morphological

transformations seen in the evolution of the tetrapod skull? We will explore the pros and cons of the different ways to model this question integrating network analysis with morphometrics.

ONTOGENY OF THE FEMUR AND FEMORAL DIMORPHISM IN A SPANISH POPULATION BASED ON TELEMETRIES AND GEOMETRIC MORPHOMETRICS

C. Rissech^{1*}, A. Pujol², J. Ventura³, D. Turbón²

1 Departament de Ciències Mèdiques, Facultat de Medicina, Universitat de Girona, Girona, Spain.

2 Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Barcelona, Spain.

3 Departament de Biologia Animal, Vegetal i Ecologia, Facultat de Biociències, Universitat Autònoma de Barcelona, Bellaterra (Cerdanyola del Vallès), Spain.

*Corresponding author e-mail address: carme.rissech@gmail.com

This paper investigates the femoral morphological development during the adolescent growth spurt. We analysed 420 left femora (240 boys and 180 girls) aged between 9 and 14 years, based on telemetries. Size and shape variation of the femur was quantified by 22 2D-landmarks and analysed in relation to age and sex using geometric morphometrics (GMM) procedures. Likewise, metrical variation of neck-shaft and bicondylar angles were determined and possible sexual dimorphism was evaluated by Student-T test. GMM analysis indicated that size and shape of the femur varied significantly with age, with males having larger dimensions than females. These changes are characterised by an increase in the robustness of the bone and shape changes in the epiphyses. During growth, the size of the greater and lesser trochanters increase and the neck-shaft angle decreases. A significant increase of distal epiphyseal dimensions was recorded, mainly in the medial condyle. In both sexes, the angular remodelling of the neck and the bicondylar regions continues until 14 years. The main age-related changes in the femur morphology of the boys correspond to the increase of the diaphyseal length and size of both trochanters, and in a lower extent to the angular remodelling of

the bone. Conversely, whereas the most important modification in girls is associated with the angular remodelling, the increase in diaphyseal length and femur size is less evident. Female and male femur each followed divergent growth trajectories. Metrical analysis indicated that males had a greater variability in neck-shaft and bicondylar angles than females. In both sexes, the angular remodelling of both angles continued after femoral growth spurt. Student-T test indicated sexual differences in both angles from 10 years of age. Our results on the timing, morphological changes and growth trajectories of the femur can be helpful in anthropological, paleoanthropological and evolutionary studies.

EVOLUTIONARY MODULARITY AND MORPHOLOGICAL INTEGRATION IN THE HAPTORAL ANCHORS STRUCTURES OF *LIGOPHORUS* SPP. (MONOGENEA, DACTYLOGYRIDAE)

A. Rodríguez-González^{1*}, R. Míguez-Lozano¹, V. Sarabeev², J.A. Balbuena¹

1 Marine Zoology Unit, Cavanilles Institute of Biodiversity and Evolutionary Biology, Science Park, University of Valencia, P.O. Box 22085, 46071 Valencia, Spain.

2 Department of Biology, Zaporizhzhia National University, Zhukovskogo 66, 69063 Zaporizhzhia, Ukraine.

*Corresponding author e-mail address: arogon5@uv.es

An important question in the study of phenotypic evolution is whether characters are independent of each other or behave and evolve as integrated modules. Morphological integration and modularity provide a powerful framework for the analysis of the evolution of morphological traits. We used geometric morphometrics and phylogenetic independent contrasts (PIC) to test four different modularity hypotheses in the haptoran anchors of 14 monogenean species of *Ligophorus*. Integration between the modular units identified was further evaluated with two-block partial least squares analysis. Roots and points represented two modules in dorsal and ventral anchors but modularity was not statistically supported when parasite phylogeny was accounted for, which may indicate convergent evolution related to host characteristics and gill morphology. By contrast, PIC revealed medial and lateral modules in ventral anchors only. Moreover and in line with previous studies, evidence for ventral and dorsal anchor pairs forming two, supporting the notion that they play different functional roles. Integration between all identified modules was strong. We conclude that there is modular structure in the anchors of *Ligophorus* spp., adaptive and phylogenetic factors acting at diffe-

rent levels account for the modularity observed, and ventral and dorsal anchors evolve as integrated modules with specific roles in attachment.

STUDY OF THE ACETABULUM OF PRIMATES USING GEOMETRIC MORPHOMETRICS

M. San Millán^{1*}, A. Kaliontzopoulou², C. Rissech³, D. Turbón¹

1 Secció de Zoologia i Antropologia, Departament Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Av. Diagonal 643, 08028, Barcelona, Spain.

2 CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas 7, 4485-661, Vairão, Vila do Conde, Portugal.

3 Unitat de Anatomia, Departament de Ciències Mèdiques, Facultat de Medicina, Universitat de Girona, 17071, Girona, Spain.

*Corresponding author e-mail address: marta.sanmillan@ub.edu

The quantification and investigation of variation in acetabular shape among primates has important implications in anthropology, as it provides a better understanding of primate evolution. Geometric morphometrics has seen new developments and advancements, becoming an excellent tool to compare biological structures. We developed a specific protocol to photograph and examine the acetabular shape of primates, through two-dimensional geometric morphometrics procedures, and tested its performance by analysing intra- and inter-observer error. Following this protocol, we examined variation across the acetabulae of 303 primates of 40 extant species, including humans. The aim was to determine how acetabular shape co-varies with locomotor behaviour, while taking both intra- and inter-specific variation into account. The results revealed that several biological factors, such as size, sex, and phylogeny, had a significant effect on acetabular shape variation. Most importantly, after accounting for shape variation based on these variables, acetabular shape was significantly different among locomotor groups. Due to their singular acetabular shape, the two most differentiated locomotor groups are leapers and slow-climbing quadrupeds. Moreover, the acetabular

shape of bipeds differed significantly from the rest of the locomotor groups. The acetabular regions that showed more shape variation among the primates analysed, were cranial, dorsal, and around both acetabular horns. Thanks to the increasing number of fossil os coxae available, the association found between shape and function provide a useful framework for future paleoanthropological analyses into the complex and poorly understood locomotor behaviour of fossil primate specimens.

LIMB CO-VARIATION AND FLUCTUATING ASYMMETRY IN THE *MUS MUSCULUS* HYBRID ZONE

N. Skrabar^{1*}, L.M. Turner¹, B. Harr¹, L.F. Pallares¹, D. Tautz¹

¹ Department for Evolutionary Genetics, Max-Planck Institute for Evolutionary Biology, August-Thienemann-Straße 2, 24306 Plön, Germany.

*Corresponding author e-mail address: skrabar@evolbio.mpg.de

Two subspecies of the house mouse—*Mus musculus musculus* and *Mus musculus domesticus*—form a narrow hybrid zone in central Europe. Hybridization may serve as a source of genetic variation for adaptive evolution. To discern whether a genetic difference is adaptive or not, it is important to consider how it influences the resulting phenotype. Natural hybrid zones have been shown to be a suitable source for exploring the genetic basis of complex traits (Turner & Harr, 2014), including skeletal characters (Pallares *et al.*, 2014).

Fore- and hind limb in tetrapods are serially homologous structures that show patterns of co-variation produced by joint genes involved in limb development. Characters that co-vary due to sharing common developmental factors are explained by morphological integration.

Furthermore, phenotypic variability could be affected (increased) through reduction of developmental stability. It can result in small random differences in two sides of a bilaterally symmetrical character of an organism that are produced by the same genome (i.e. fluctuating asymmetry).

In this study, we investigate co-variation between and within fore- and hind limbs and fluctuating asymmetry in samples from the mouse hybrid

zone using 3D landmarks and geometric morphometrics. Further, we are performing a genome-wide association study (GWAS) in first generation lab-bred offspring of wild-caught hybrid mice to identify loci associated with limb variation. We will report on the first results of this analysis.

Pallares, L.F., Harr, B., Turner, L.M., Tautz, D. (2014). Use of a natural hybrid zone for genomewide association mapping of craniofacial traits in the house mouse. *Molecular Ecology* 23, 5756-5770.

Turner, L.M., Harr, B. (2014). Genome-wide mapping in a house mouse hybrid zone reveals hybrid sterility loci and Dobzhansky-Muller interactions. *eLife* 3, e02504.

GRASS PHYTOLITH SHAPE: A KEY TO EVOLUTION AND PALEOECOLOGY OF GRASSES AND GRASSLANDS

C.A.E. Strömberg^{1,2*}, E. Abouafia³, W.H. Brightly^{1,2}, C. Crifò^{1,2}, B. McManus³, C. O'Keefe¹, A. Schorr¹,
A. Senske¹

1 Department of Biology, University of Washington, Seattle, WA 98195, USA.

2 Burke Museum of Natural History and Culture, University of Washington, Seattle, WA 98195, USA.

3 Department of Earth and Space Sciences, University of Washington, Seattle, WA 98195, USA.

*Corresponding author e-mail address: caestrom@uw.edu

Phytoliths are microscopic silica bodies that are produced in the tissues of many vascular plants. Grasses produce a diverse range of phytolith shapes, so-called grass silica short cells (GSSC) that distinguish them from phytoliths produced by other plants. It has long been known that GSSC shapes broadly reflect grass classification, and these differences have been used in paleontology and archaeology to reconstruct evolutionary divergences within the grass family (Poaceae), grass community composition in ancient (Cretaceous-Cenozoic) ecosystems, and human domestication of grasses. Nevertheless, it remains unclear just how well GSSC morphology reflects relatedness among grasses in light of the new, molecular-based Poaceae phylogenies, which have drastically altered traditional views of grass relationships. In addition, previous studies have focused mainly on two-dimensional GSSC shape categories, rather than trying to assess three-dimensional shape quantitatively.

Here we attempt to establish a phylogenetically-based, morphological phytolith key that takes into account (1) the relative abundances of GSSC shape categories (rondel, pyramidal, crenate/polylobate, saddle, bilobate, cross) produced by grass species, and (2) the detailed three-dimensional

shape variation within these categories. To do so, we study phytolith assemblages extracted from modern grass species from across the Poaceae phylogeny. For each grass species, we first classify each GSSC into a shape category and calculate the relative abundance distribution of these categories. Second, we use high-resolution light-microscopy images to collect landmark- and semilandmark data to quantitatively compare shapes within each shape category. Preliminary data indicate that both distribution of GSSC shape categories and detailed variation within shape categories provide at least coarse distinctions between clades. Work is ongoing to refine the method and add taxa to determine the phylogenetic resolution of GSSC phytoliths and test hypotheses about GSSC shape evolution.

**COMPREHENSIVE MORPHOMETRIC ANALYSIS OF WILD AND FARMED GILTHEAD SEABREAM
(*SPARUS AURATA*, L. 1758) IN THE EASTERN ADRIATIC SEA**

I. Talijančić^{1*}, T. Šegvić-Bubić¹, L. Grubišić¹, I. Katavić¹, I. Žužul¹

1 Institute of Oceanography and Fisheries, Šetalište I. Meštrovića 63, 21000 Split, Croatia.

*Corresponding author e-mail address: talijan@izor.hr

The expansion of modern aquaculture industry of gilthead sea bream *Sparus aurata* and European sea bass *Dicentrarchus labrax* introduced new impacts on biota in form of escape of domesticated individuals from farms and their dispersal into wild fish populations. Interaction of wild and farmed fish has led to scenarios with negative ecological and genetic consequences such as increased predation and competition for specific habitat and food resources and unfavourable gene flows between reared and wild individuals. Escape events in the last decade significantly increased the biomass contribution of escapees to local habitats, and thus fisheries landings across Mediterranean, which led to intentional mislabelling of farmed fish as wild on the markets because of the difficulty to distinguish them.

In this study, we evaluate possible ecological impacts of escaped farmed gilthead sea bream in the eastern Adriatic Sea using morphometric features of body shape, which proved to be a fast, accurate and cost-effective diagnostic tool for rapid assessment in the field. A combination of classical measurement scheme, truss network system, geometric morphometric and condition factor index is used in order to trace possible escapees among

wild populations through investigation of morphological similarity/dissimilarity between eleven wild and three farmed groups of different stock origin.

We discuss the morphometric results of these three different methods used for population discrimination in order to provide better guidelines for fish origin assessment and quantification of escapees in wild. The proposed tool is highly important for aquaculture industry (recapture strategy) as well for environmental managers (genetic diversity protection of native populations).

ADDING PHYLOGENETIC TREES TO IMPROVE VIRTUAL RETRODEFORMATION: CERCOPITHECIDAE AS A TEST CASE

M. Tallman^{1,2*}, N. Amenta³, E. Delson^{2,4}, S.R. Frost^{2,5}, D. Ghosh⁶, F.J. Rohlf^{2,4,7}

1 Grand Valley State University, Ilandale, MI, USA.

2 NYCEP Morphometrics Group, New York, NY, USA.

3 University of California-Davis, Davis, CA, USA.

4 College and Graduate Center/CUNY, American Museum of Natural History, NYCEP, USA.

5 University of Oregon, Eugene, OR, USA.

6 Stratovan Corp, Sacramento, CA, USA.

7 Stony Brook University, Stony Brook, NY, USA.

*Corresponding author e-mail address: ltallman@gmail.com

Three-dimensional shape analysis is increasingly used to answer questions about functional morphology, paleoecology and phylogeny of fossil taxa. Diagenetic shape change is a major obstacle for the use of geometric morphometrics (as well as more standard analytical approaches). Retrodeformation is the process of returning a deformed fossil to its antemortem – or “pre-death” – shape. The techniques of simple reflection and averaging and the more recently published approach of algorithmic symmetrization both adjust for asymmetrical deformation. Symmetrical deformation, however, remains a problem. Here we present a potential solution for addressing symmetrical deformation in fossil crania using three-dimensional morphometric data in combination with assumed phylogenetic relationships to create hypotheses for antemortem shape.

Dense patches of semilandmarks were collected on surface scans of the crania of undeformed extant and fossil cercopithecids and mapped onto a composite molecular phylogenetic tree with estimated divergence dates. Hypothetical landmark configurations representing all ancestral nodes and transformations along branches were calculated using a squared-change parsimony model of (Brow-

nian-motion) evolution. Two mechanically deformed casts of *Papio hamadryas kindae* crania of known antemortem shape were first retrodeformed with algorithmic symmetrization (as in our previous work) and then fit onto the tree by finding the place – or places – where Procrustes distance was minimized.

Three-dimensional models were generated based on the landmark configurations at those places and were used as templates to further correct the symmetrical deformation present in the crania yielding a series of hypothetical reconstructions of antemortem shape. Principal component analyses of a broad sample of extant cercopithecids indicate that the hypothetical reconstructions fall within the range of extant variation of *P. h. kindae*. Permutation tests of pairwise Procrustes distances among the extant taxa and retrodeformed models indicate that the retrodeformed specimens are significantly more similar to other *P. h. kindae* than to members of any other taxon.

DENTAL MORPHOMETRIC EVOLUTION IN RECENT SPANISH POPULATIONS

S. Torrijó-Boix^{1*}, A. Romero¹

¹ Departamento de Biotecnología, Universidad de Alicante, 99 E-03080 Alicante, Spain.

*Corresponding author e-mail address: sipunculido@gmail.com

Teeth in modern humans differ in morphological traits. Quantitative genetics suggest that dental phenotypic variance among populations is influenced by random processes of founder effect and genetic drift. However, we have little evidence about the effect of ecological and nutritional factors in the ontogenetic process and expression of dental morphological characters. Here, we analyzed first maxillary molars (M^1) by means of geometric morphometrics to quantify crown morphology and size in two diachronic Spanish populations from cemetery-derived (19th century, $n=45$) and contemporary (21st century, $n=39$) individuals. Occlusal surface digital images were captured from high-resolution replicas. Dental shape and size (CS) were extracted from the landmark configurations using generalized least-square Procrustes superimposition and subjected to multivariate analysis. Results show that both populations display significant shape-size variation. Size-adjusted shape coordinates (ANCOVA) exhibited differences between populations ($P<0.01$) especially when the present-day subjects were compared to older ancestral molar complexity smaller in size. Further, cross-validated discriminant functions showed 90% of study sub-

jects correctly classified. In contrast to evolutionary dental reduction models, our findings suggest that current populations may have developed greater variability in crown morphology as an inverse plastic response to micro-evolutionary and historical events, since tooth size is related to health weakening and shape as a measure of biological affinities. Spanish people covered gradually their nutritional requirements after the 60's, when an increase in meat and milk products occur in dietary intake. Therefore, the greater bio-availability of calcium suggests changes in developmental tooth processes and pleiotropic effects. A single selective pressure would result in differential dental morphological trends.

MODELLING FLORAL EVOLUTION IN *PELARGONIUM* (GERANIACEAE)S.J. van de Kerke^{1*}, C. Broek¹, L. Schat¹, E. Schranz¹, F.T. Bakker¹

1 Biosystematics Group, Wageningen University, Droevendaalsesteeg 1, 6708 PB, Wageningen, The Netherlands.

*Corresponding author e-mail address: sara.vandekerke@wur.nl

Floral evolution in the predominantly South African *Pelargonium* clade (Geraniaceae) has resulted in a broad spectrum of shapes and syndromes, representing the use of several groups of pollinators. Whether pollinator switches may have driven speciation and hence clade size differences in this group, remains to be tested (although preliminary data on nectar spur lengths indicates it does).

In this study, we will focus on the evolution of floral shape and its relation to clade size and speciation by morphometrically modelling floral diversity in *Pelargonium*. Floral morphological differences among *Pelargonium* species need to be quantified in order to assess transitions and trends in, for instance, corolla shape, spur shape and length, stamen orientation etc., and in order to identify morphological equilibria and, possibly, 'avoided shapes'. We will use both 3D landmark geometric modelling as well as morphogenesis modelling of selected series and clades of species within the *Pelargonium*. Results will be placed in a phylogenetic framework to test whether different aspects of floral evolution have evolved in concert or independently, and how they may have driven speciation in this clade.

Here, we present preliminary results of a geometric morphometric analysis on corolla shape for a number of *Pelargonium* species, based on a photogrammetry approach.

RELIABILITY OF ESTIMATING PHYLOGENIES FROM SHAPE AND SIMILAR MULTIDIMENSIONAL DATA

C. Varón-González^{1*}, S. Whelan², C.P. Klingenberg¹

1 Faculty of Life Sciences, University of Manchester, Michael Smith Building, Oxford Road, Manchester M13 9PT, United Kingdom.

2 Dept. of Evolutionary Biology, EBC, Uppsala University, Norbyägen 18D, 75236 Uppsala, Sweden.

*Corresponding author e-mail address: ceferino.vg@gmail.com

In recent years, there has been some controversy about whether multidimensional data such as geometric morphometric data on shape or information on gene expression can be used for estimating phylogenies. This study addresses this question with simulations of evolution in multidimensional phenotype spaces. The simulations use the four-taxon case, where there are just three possible tree topologies, and a comprehensive scheme to cover different combinations of branch lengths. Under an evolutionary model of isotropic Brownian motion, phylogeny can be estimated reliably if dimensionality is high. If phenotypic variation is integrated so that most variation is concentrated in one or a few dimensions, the reliability of phylogenetic estimates is seriously reduced, corresponding to the reduced dimensionality of the data. Taking into account integration by using Mahalanobis distance in estimating phylogenies can restore phylogenetic reliability only in part, depending on the sample size used to estimate patterns of integration. Evolutionary models with stabilizing selection produce unreliable estimates, which are little better than picking a phylogenetic tree at random. A best-case scenario with an evolutionary model of mutual repulsion among taxa produces reliable estimates of

phylogeny, but cannot be considered a realistic model of evolution in natural clades. Overall, the simulations suggest that multidimensional data, under plausible evolutionary models, do not produce reliable estimates of phylogeny.

ONTOGENETIC CHANGES IN SCAPULAR FORM IN FOSSORIAL WATER VOLES

J. Ventura^{1*}, J. Martínez-Vargas¹, F. Muñoz-Muñoz¹

1 Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia, Facultat de Biociències, Universitat Autònoma de Barcelona, Avinguda de l'Eix Central, Edifici C, E-08193 Bellaterra (Cerdanyola del Vallès), Spain.

*Corresponding author e-mail address: jacint.ventura.queija@uab.cat

In order to provide new information to disentangle the complex interaction between ontogenetic and functional determinants of shape in the mammalian scapula, we analysed the postnatal growth and morphological integration of this structure in *Arvicola scherman monticola*, a water vole taxon with fossorial locomotion. Scapulae belonging to 107 collection specimens assigned to five classes of relative age were studied. Seventeen bi-dimensional landmarks were digitised on images corresponding to the dorsal side of this structure. Program "MorphoJ" (version 1.06d) was used for geometric morphometric analyses. Scapular size and shape differed significantly between age classes but not between sexes. Twenty-six per cent of shape variation was explained by size. After removing the effect of size, shape differences related to age remained significant. Canonical variate analysis showed that the main changes during postnatal ontogeny consisted in a general narrowing of the glenoid-acromion region, a caudal expansion of the infrapinuous fossa and a broadening of the supraspinous fossa. Most pronounced modifications occur during the first ten weeks of postnatal life. Once individuals reach sexual maturity, scapular shape changes are relatively moderate. Neverthe-

less, when a canonical discriminant analysis was applied on individuals of age classes 4 and 5, noticeable age-related differences in scapular shape were detected. Considering the insertion areas and function of the scapular muscles, these differences can be attributed to the remodeling of the scapula caused by the intense digging activity during adulthood. Analyses of RV coefficient revealed two significant modules: glenoid region-coracoid-acromion and lamina-scapular spine. This pattern is concordant with the ossification process of the scapula, which indicates that the phenotypic integration pattern associated with development is not significantly altered by function.

MODULARITY OR INTEGRATION OR BOTH? 3D ANALYSIS OF 21 GENERA OF FROGS DEMONSTRATES PHYLOGENETIC CONSERVATISM IN SKULLS AND LABILITY IN LIMBS

M. Vidal-García^{1*}, J.S. Keogh¹

¹ Evolution, Ecology & Genetics, Research School of Biology, The Australian National University, Canberra, ACT, Australia.

*Corresponding author e-mail address: marta.vidalgarcia@anu.edu.au

Quantifying morphological diversification across taxa can provide valuable insight into evolutionary processes, yet the its complexities can make it difficult to identify appropriate units for evaluation. One of the challenges in this field is distinguishing between the morphological integration and modularity hypotheses, where morphological evolution of different structures is explained either by co-variation between them, or by independent evolution respectively. Here we used a 3D geometric morphometric approach with x-ray micro CT scan data of the skull and bones of fore-limbs and hind-limbs of representative species from all 21 genera of the ancient Australo-Papuan myobatrachid frogs, and analysed their shape both as a set of distinct modules and as a multi-modular integrative structure. We then tested three questions: (i) is morphological disparity similar between the two major subfamilies, (ii) do skulls and limbs show different levels of integration, and (iii) is shape variation correlated with locomotion, burrowing behavior, and ecology. We found that morphological disparity was similar in both species-rich subfamilies. Skull shape diversity was phylogenetically conserved, whereas limb shape was more associated with ecology, particularly in fossorial species. Mor-

phological differences between different limb bones were highly correlated, depicting high morphological integration. In contrast, overall limb and skull shape displayed semi-independence in morphological evolution, favouring the modularity hypothesis. Our results show how form can be correlated with function, with the evolution of limb shape being driven by selective pressures imposed by the environment and functional requirements of locomotion and behaviour. Our results also illustrate how morphological evolution can display varying degrees of independence across different modules, and that quantifying this is crucial in order to make accurate predictions of complex evolutionary processes.

RIGID ROTATION OF THREE-DIMENSIONAL STRUCTURES: STANDARDISED SPINNING PROCEDURE FOR COMBINED SHAPE ANALYSES OF ARTICULATED 3D STRUCTURES WITH APPLICATION FOR GEOMETRIC MORPHOMETRICS

M. Vidal-García^{1*}, L. Bandara², J.S. Keogh¹

1 Evolution, Ecology & Genetics, Research School of Biology, The Australian National University, Canberra, ACT, Australia.

2 Department of Mathematical Sciences, Chalmers University of Technology and University of Gothenburg, Gothenburg, Sweden.

*Corresponding author e-mail address: marta.vidalgarcia@anu.edu.au

The quantification of complex morphological patterns typically involves comprehensive shape and size analyses, usually obtained by gathering morphological data from all the structures that capture the phenotypic diversity in an organism or object. Articulated structures are a critical component of overall phenotypic diversity, but data gathered from these structures is difficult to incorporate in to modern analyses. While there are already described methods for analysing shape variation in articulated structures in Two-Dimensional (2D) space, these methods do not work in 3D, a rapidly growing area of capability and research. Here we describe a simple geometric rigid rotation approach that removes the effect of random translation and rotations, enabling the morphological analysis of 3D articulated structures. Our method is based on Cartesian coordinates in 3D space so it can be applied to any morphometric problem that also uses 3D coordinates (e.g. spherical harmonics). We demonstrate the method by applying it to a landmark-based data set for analysing shape variation using geometric morphometrics. This method can be easily implemented in the commonly used software programs Geomorph and MorphoJ. We believe our method will be a valua-

ble tool for 3D morphological analyses in articulated structures by allowing an exhaustive examination of shape and size diversity.



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Campus de la UBA
Mòdul ICP (Espina 83 bis parell)
Universitat Autònoma de Barcelona
0819 Bellaterra (Cerdanyola del Vallés) Barcelona

Tel. 93 586 83 37



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