UFRGS
UNIVERSIDADE FEDERAL
DO RIO GRANDE DO SUL

ONTOGENIA CRANIANA COMPARADA DE *Arctocephalus australis*, *Callorhinus ursinus* E *Otaria byronia* (OTARIIDAE: PINNIPEDIA)

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"ES PORQUE APRENDÍ LUCHANDO QUE MI DEBER DE VIDA ES PROPAGAR LA ALEGRÍA".
(PABLO NERUDA)

THUNDER ROAD
(Bruce Springsteen, 1975)

The screen door slams
Mary´s dress waves
Like a vision she dances across the porch
As the radio plays
Roy Orbinson singing for the lonely
Hey that´s me and I want you only
Don´t turn me home again
I just can´t face myself alone again
Don´t run back inside
Darling you know just what I´m here for
So you´re scared and you´re thinkng
That maybe we ain´t that young anymore
Show a little faith, there´s magic in the night
You ain´t a beauty, but hey you´re alright
Oh and that´s alright with me

You can hide ´neath your covers
And study your pain
Make crosses from your lovers
Throw roses in the rain
Waste your summer praying in vain
For a savior to rise from these streets
Well now I´m no hero
That´s understood
All the redemption I can offer, girl
Is beneath this dirty hood
With a chance to make it good somehow
Hey what else can we do now?
Except rool down the window
And let the wind blow back your hair
Well the night´s busting open
These two lanes will take us anywhere
We got one last cane to make it real
To trade in these wings on some wheels

Climb in back
Heaven´s waiting on down the tracks
Oh oh come take my hand
Riding out tonight to chase the promised land
Oh oh Thunder Road, oh Thunder Road
Oh Thunder Road,
Lying out there like a killer in the sun
Hey Know it´s late, we can make it if we run
Oh Thunder Road, sit tight take hold
Thunder Road
When I got this guitar
And I learned how to make it talk
And my car´s out back
If you´re ready to take that long walk
From your front porch to my front seat
The door´s open but the ride it ain´t free
And I know you´re lonely
For words that I ain´t spoken
But tonight we´ll free
All the promises´ll be broken
There were ghost in the eyes
Of all the boys you sent away
They haunt this dusty beach road
In the skeleton frames of burned out Chevrolets
They scream your name at night in the street
Your graduation gown lies in rags at their feet
And in the lonely cool before dawn
You hear their engines roaring on
But when you get to the porch they´re gone
On the wind, so Mary climb in
It´s a town full of losers
And I´m pulling out of here to win.

SUMÁRIO

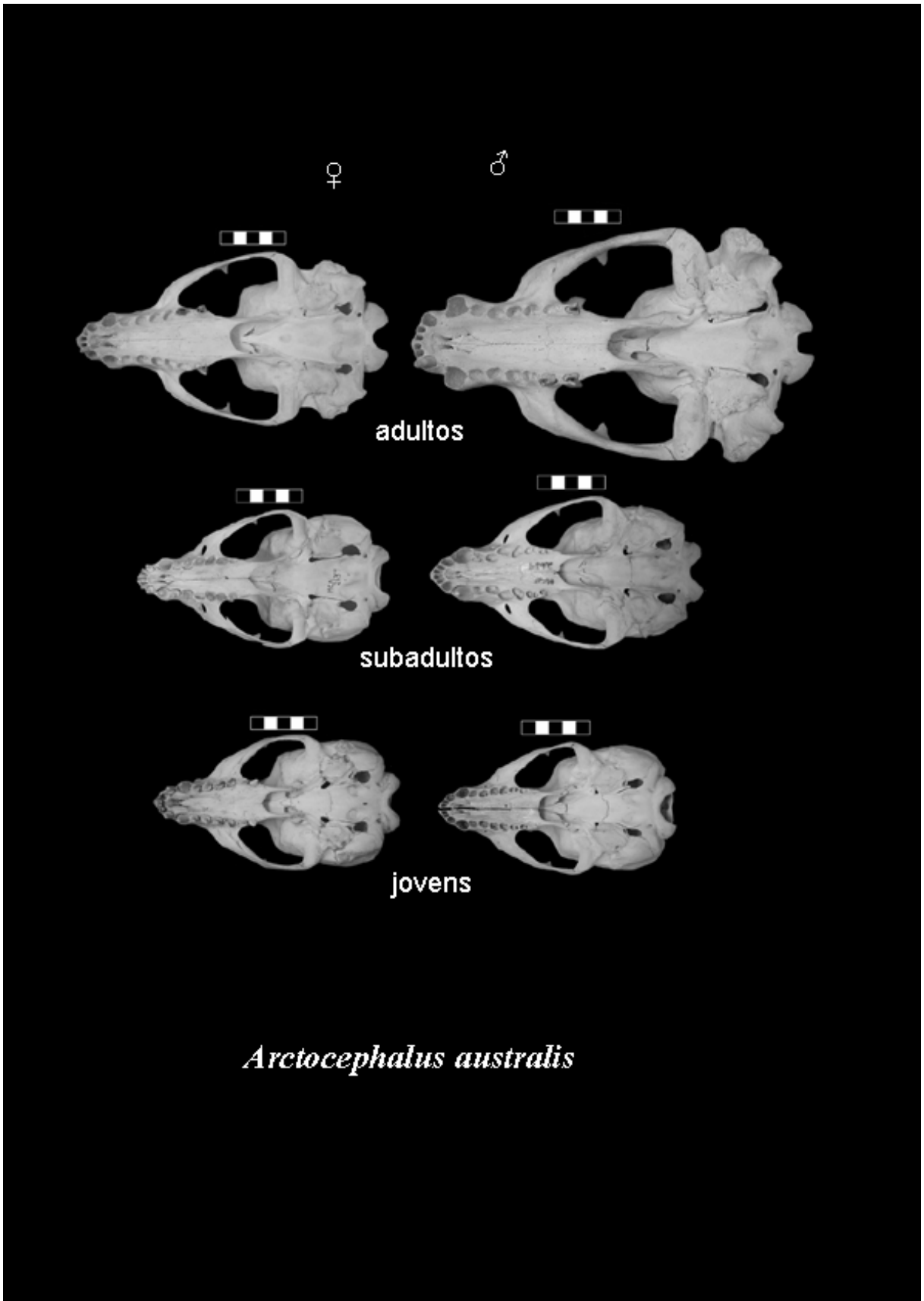
APRESENTAÇÃO E CONSIDERAÇÕES GERAIS

O presente trabalho está configurado de modo que os resultados são apresentados e discutidos em manuscritos independentes, com vistas a posterior publicação. Entretanto, contém também capítulos mais genéricos, que contextualizam a problemática central do desenvolvimento craniano das espécies de otarídeos enfocadas (INTRODUÇÃO); abordam aspectos mais gerais das metodologias empregadas ao longo de todo este estudo (MATERIAS & MÉTODOS) ou ainda, dão um "fechamento" do tema abordado (CONCLUSÕES), onde são retomados sucintamente os pontos centrais, sedimentando então, o arcabouço geral deste estudo.

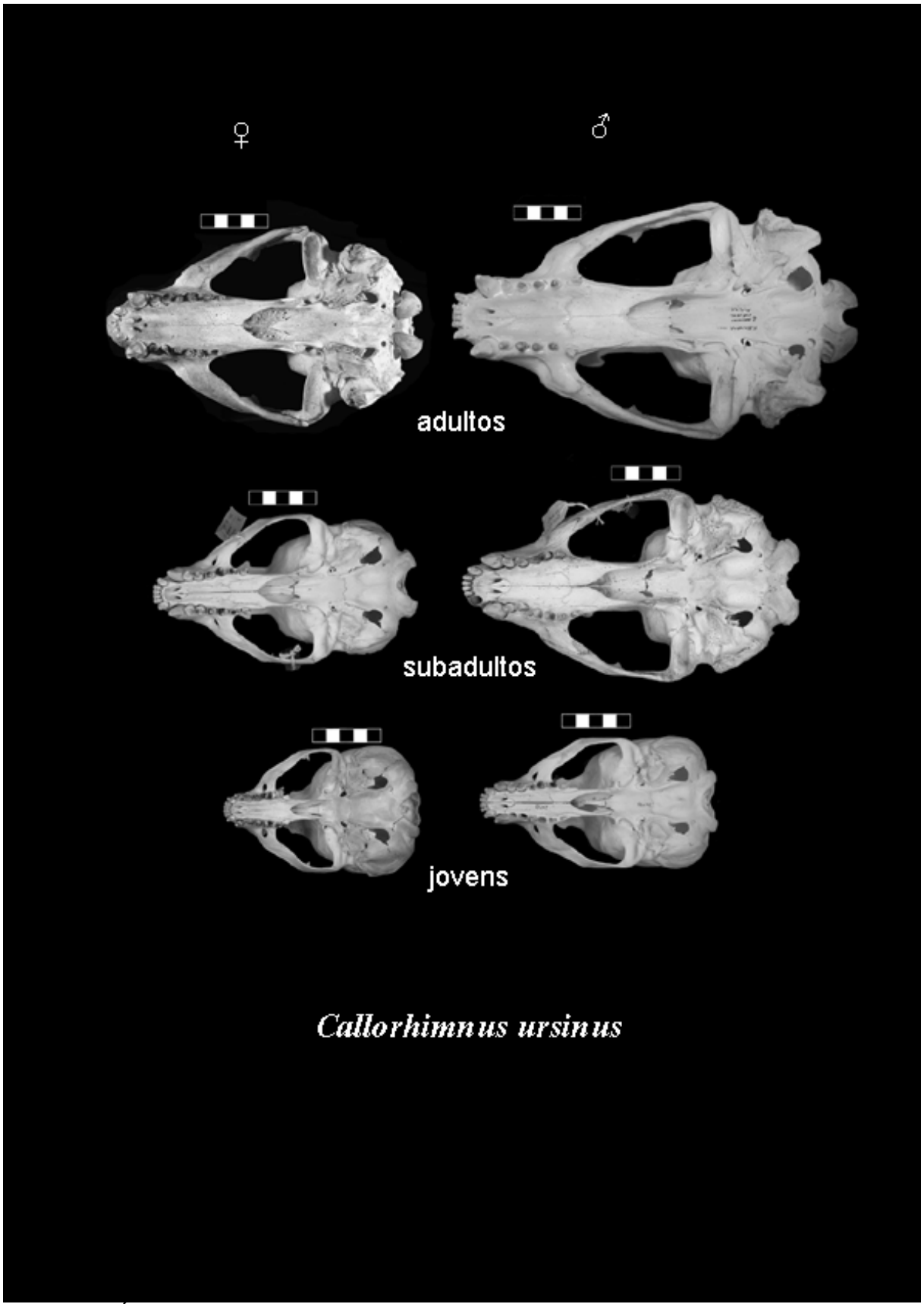
Apresentam-se um total de cinco manuscritos que se desenvolvem sempre sob a ótica de um estudo comparativo. O primeiro utiliza exclusivamente análises multivariadas de distâncias lineares objetivando, basicamente, o estudo comparado dos padrões alométricos das diferentes espécies e sexos, ao longo do desenvolvimento. O segundo capítulo trata da descrição dos padrões de crescimento e desenvolvimento do crânio, os quais são avaliados empregando-se morfometria geométrica e tradicional (medidas lineares). Já os três últimos fazem uso, exclusivamente, de técnicas de morfometria geométrica. O primeiro destes (Capítulo 3), trata essencialmente da descrição das relações morfogenéticas do dimorfismo sexual. O Capítulo 4 discute quais padrões de mudanças na ontogenia estariam atuando na evolução dos Otariidae (considerando as espécies examinadas) e o último (Capítulo 5) está focado nos conceitos de nível e padrão de Disparidade (total e parcial) e suas conseqüências na morfogênese pós-natal do crânio destas espécies.

ABSTRACT

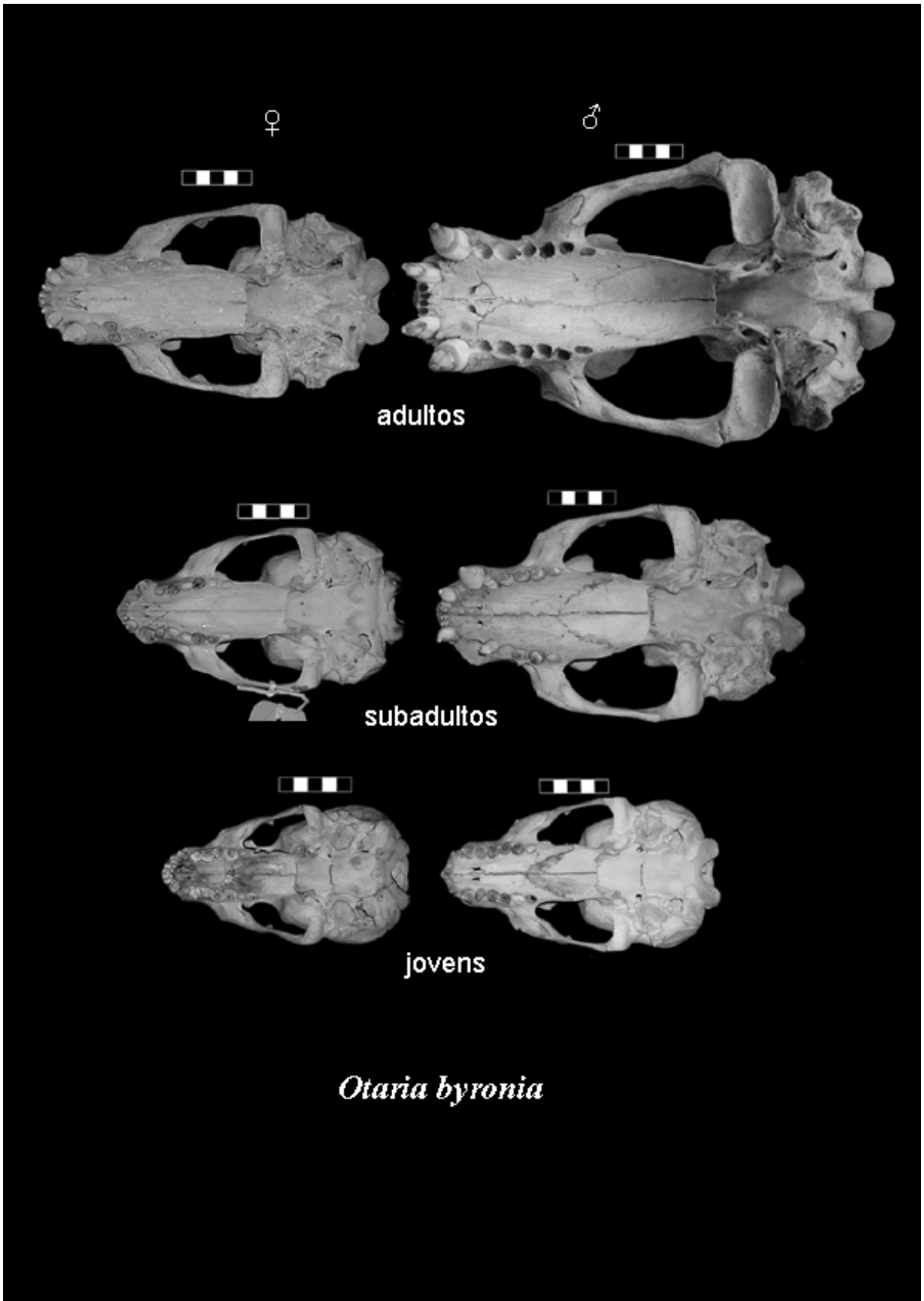
The search for mechanisms that can generate major morphological changes has led to the study of ontogeny, in part because some kinds of modifications of ontogenies seem an excelent way to generate major phenotypic change. We focus here on *Arctocephlaus australis*, *Callorhinus ursinus* and *Otaria byronia* with the aim of contributing to the understanding of the origin, structure and temporal patterns of otarid morphological diversity. The pattern of change in shape during postnatal development in otarid skull was studied and described by geometric and traditional morphometrics. Our aims are: to compare the skull ontogeny of the species invocated in identifying and in describing shape alterations in the skull; to evaluate and to describe comparatively the sexual dimorphism and disparity during the ontogeny; to study the covariance between size and shape in relationship with age-groups; to investigate the changes in the ontogeny and their relationships with the evolution of the Otariidae Family; to analyze the conservation of ontogenetic trajectories over time, between sexes and among species; to characterize growth trajectories and to compare them among taxa with respect to isometry; to describe the parameters of growth and development of the focused species and to compare the two different approaches employed. Using traditional morphometrics, the allometry vectors for all species were significantly different from isometry. Dimorphism in the allometric vector is observed only in *O. byonia* and the difference between males and females of the fur seals are related with adult body size. The comparisons species/sex groups revealed similar vectors (any significant shape disassociation are verified in the inter-specific analyzes), suggesting lower plasticity of the ontogenies. Using geometrical methods, the dimorphism is more conspicuous in adult shapes but this is not true for the level of disparity between sexes of *O. byronia*. Although that dimorphism is linked with size this is not only a question of scaling or allometry (which is present in the morphogenesis of all species, especially in *O. byronia*). Additionally, the slopes of changes in shape related with size increase are different in *A. australis* and *O. byronia*, but are equal in *C. ursinus*, which is the smaller species. We suggest post-displacement as one of the factors that could have acted in the origin of the sexual dimorphism in the skull of *C. ursinus*. Heterochrony, perhaps is present in the roots of the modifications suffered by the ontogeny of *A. australis* and *O. byronia* too, considering the differences in the rates of development between the sexes of both species (and overall in *O. byronia*), but surely repatterning allometric is involved too in these cases. We verified that ontogenies can not be summarized by a single linear vector in any analyzed group, where *C. ursinus* ontogeny is the more linear and *O. byronia* the more multi-dimensional species among the 3 that we had examined. Shape changes in the otarids studied here are more related with size than with age and any of the species share a common growth allometry or a common ontogenetic trajectory/pattern. In the same way, shapes at onset or offset are not the same in any case. When the three species are pooled together, initial shapes are always very different among the species and the distances between shapes increase with time almost independently from size. On the other hand, when the complete samples are considered, all the ontogenetic trajectories are significantly different in the directions of the allometric vectors during ontogeny. Ontogenetic trajectories differ significantly among almost all the pairs compared, except for the trajectories of *A. australis* and *C. ursinus* males. They are no more different than expected by chance considering the range of angles within each sample. A similar pattern is found when the subadults are compared between pairs of species and when we compare adult males of *A. australis* with adult males of *O. byronia*. The juveniles are no more different than expected by chance (correlation between ontogenies in that phase is equal to one), excepti between *C. ursinus* and *O. byronia*. The ontogenetic trajectory of *C. ursinus* is the shorter and of *O. byronia* is the longer being almost three times longer than the former. *A. australis* has an intermediary length of ontogenetic trajectory. For the sample comprising all three species disparity increase significantly over ontogeny since the disparity of the adults is near the two times of the disparity between juveniles. For any ontogenetic stage, *O. byronia* is the species that contributes for the disparity of the all group, followed by *C. ursinus*. When we consider the three species together, the pattern of disparity do not change a lot during ontogeny. Ontogenies examined herein are clearly not constrained and perhaps the differences in patterns have additive effects in the differentiation of the ontogenies. Whether ontogenetic trajectories are linear or curve could be a function of developmental timing or more specifically it could depend on the age at which allometries stabilize in post-natal ontogenies. Otherwise, the amount of differences between species in the ontogenies is in agreement with the phylogenetic relationships. Finally, we addressed basically the following questions: Is onset time the same in the species? Is offset time the same in these species? Does growth rate differ between the species. The answer to those questions could be summarized by the conclusion. but we conclude that the changes in otarids skull ontogenies had occurred in spatial and temporal terms.



PRANCHA NÚMERO 1. Séria ontogenética do crânio de machos e fêmeas de *Arctocephalus australis* em vista ventral.



PRANCHA NÚMERO 2. Séria ontogenética do crânio de machos e fêmeas de *Callorhinus ursinus* em vista ventral.



PRANCHA NÚMERO 3. Séria ontogenética do crânio de machos e fêmeas de *Otaria byronia* em vista ventral.

1 INTRODUÇÃO

1.1. OS PINNIPEDIA

Os Pinnipedia alternam sua vida entre terra (reprodução, muda e descanso) e mar (relações tróficas). O nome que define este grupo tem origem no latim, significando “pés em forma de nadadeira”. As 33 espécies viventes são classificadas em três famílias: Otariidae (14 espécies), Phocidae (18 espécies) e Odobenidae (1 espécie).

O padrão corporal dos pinipédios apresenta inúmeras adaptações ao ambiente aquático, sendo as mais conspícuas o corpo fusiforme, membros em forma de nadadeiras com os joelhos e cotovelos muito próximos ao corpo, cauda vestigial e espessa capa de gordura subepidérmica (WALKER *et al*., 1964). A dentição dos Pinnipedia apresenta uma tendência à homodontia e à redução no número de dentes.

Os pinipédios são animais de porte médio a grande, possuem olhos grandes e audição aguçada, com modificações fisiológicas e anatômicas para a percepção do som quando submersos (MOORE, 1981). Tratam-se de animais altamente gregários, constituindo grandes colônias em praias e ilhas. Em acréscimo, exibem níveis baixos de polimorfismo genético (LENTO *et al*., 1997).

Diversidade e abundância deste grupo são maiores no Atlântico, norte do Pacífico e nas bordas do continente antártico. Estão ausentes apenas no oeste do Oceano Indo-pacífico oeste, que apresenta uma história contínua de águas quentes desde o início do Terciário (DAVIES, 1958). No Brasil, os pinipédios são comuns no Estado do Rio Grande do Sul, especialmente os gêneros *Otaria* Péron, 1816 e *Arctocephalus* Geoffroy Saint-Hilaire & Cuvier, 1826.

A classificação dos Pinnipedia traz consigo diversas questões polêmicas a respeito da evolução e filogenia do grupo. FLOWER (1869) estabeleceu a teoria da origem bifilética para os pinipédios (Otariidae e Odobenidae teriam derivado dos Ursidae e os Phocidae teriam evoluído a partir dos Mustelidae). Essa idéia predominou até décadas atrás, baseada em caráteres basicranianos e na biogeografia/paleozoogeografia. Desde então, inúmeros arranjos sistemáticos têm sido propostos, sendo que até hoje não há consenso sobre as relações genealógicas dos pinipédios e destes com os demais Carnivora. Com efeito, a evolução dos pinipédios é enigmática tanto no que concerne a sua origem a partir dos carnívoros terrestres como no que se refere às relações entre as três famílias (ÁRNASON et al, 1994).

Até os anos oitenta do século passado, o monofiletismo não havia obtido maior aceitação, mas a partir dos trabalhos de osteologia craniana e pós-craniana de WYSS (1987, 1988) o debate tomou novos rumos. Segundo este autor, um ancestral fissípedo (Canoidea) não seria incompatível com a seqüência de eventos de rupturas e formação de conexões no Mar de Bering durante o Oligoceno e o Eoceno, o que teria influído na diferenciação dos pinipédios. A descoberta de novas espécies fósseis tem sido decisiva para corroborar a teoria monofilética, que é adotada no presente trabalho (Fig. 1).

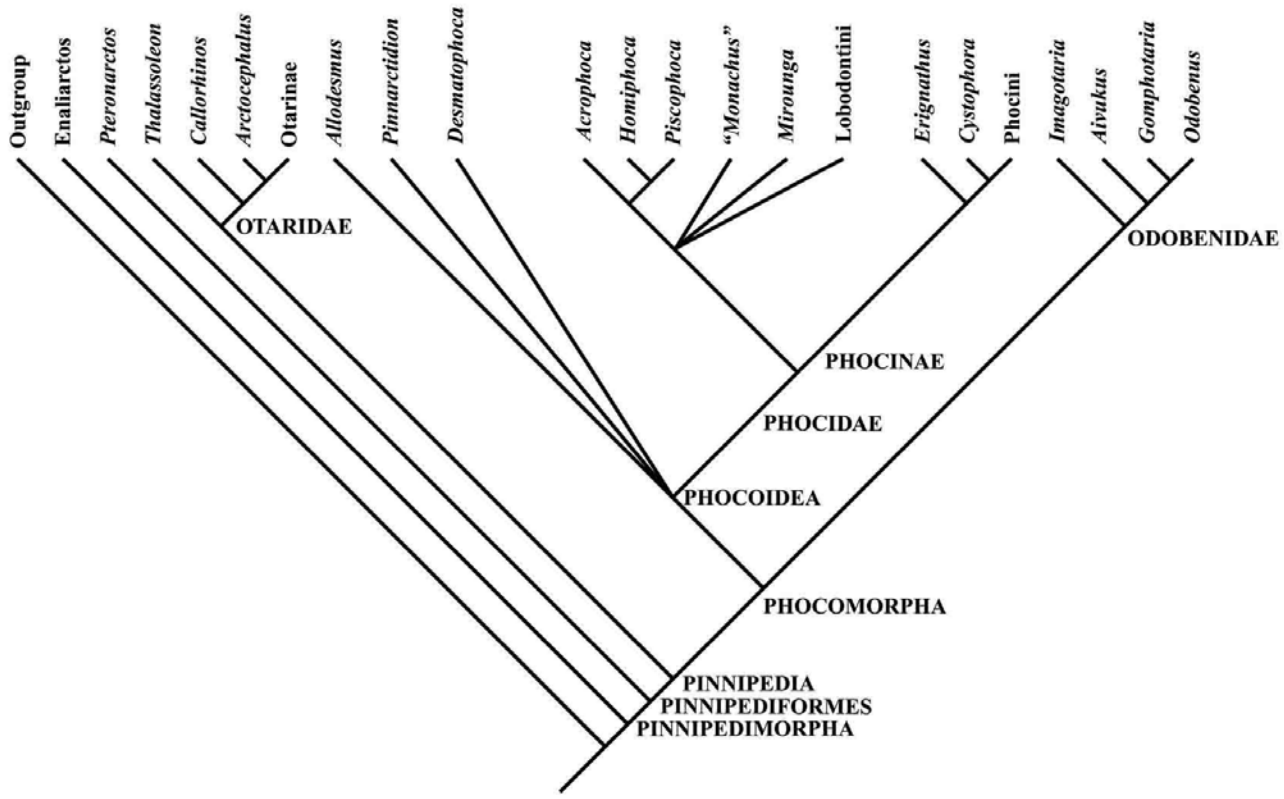


Figura 1. Filogenia dos Pinnipedimorpha modificada de BERTA & SUMICH, 1999.

1.1.1. OS OTARIIDAE GILL, 1866

Segundo SIVERTSEN (1954), a família Otariidae do ponto de vista sistemático é uma das mais complexas entre os carnívoros. Atualmente, os Otariidae compreendem sete gêneros, a saber: *Arctocephalus* Geoffroy Saint-Hylaire & Cuvier, 1826, *Callorhinus* Gray, 1859 , *Eumetopias* Gill, 1866, *Neophoca* Gray, 1866, *Otaria* Péron, 1816, *Phocartos* Petters, 1866 e *Zalophus* Gill, 1866. Apenas o gênero *Arctocephalus* não é monoespecífico, compreendendo oito espécies. Três espécies ocorrem no Rio Grande do Sul: *A. australis* Zimmerman, 1783, *A. tropicalis* Gray, 1872 e *A. gazella* Peters, 1875 (SIMÕES-LOPES *et. al.*, 1995).

Representantes dessa família ocorrem no Oceano Pacífico, Atlântico Sul e sul do Oceano Índico, incluindo, portanto, regiões árticas, temperadas e subtropicais (DREHMER, 1994). O registro fóssil é muito restrito (OLIVEIRA & DREHMER, 1998; DREHMER & RIBEIRO, 1998), sendo que o Pacífico nordeste é considerado como o centro de origem da família (REPENNING *et al*., 1979). A ampla distribuição geográfica deriva de dispersões e radiações mais recentes e observa-se que *Callorhinus* mantém-se restrito ao Hemisfério norte, mas leões-marinhos e o gênero *Arctocephalus* dispersaram em ambos os hemisférios equatorianos.

Esta família caracteriza-se externamente por apresentar nadadeiras anteriores grandes e em forma de remo, presença de ouvido externo pequeno e cartilaginoso (de onde deriva seu nome, do Grego *ótos* = orelha), nadadeiras posteriores que podem dirigir-se anteriormente (participando do deslocamento em terra)

e por machos muito maiores que as fêmeas (DREHMER, 1994; BRUNNER, 1998a; b).

Os otarídeos são poligâmicos e seu período de gestação é de aproximadamente um ano, sendo o período reprodutivo no verão. A fórmula dentária normal é I3/ 2 C1/1 1PM4/4 M1,2ou3/1 (total=34 ou 38) (WALKER, 1964).

No que concerne à osteologia, pode-se citar como características dessa família o processo supra-orbital do frontal em forma de plataforma, frontais que se interpõem entre os nasais, presença do canal do alisfenóide, uma rugosidade secundária na escápula e forames vertebrais alargados. O calcâneo dos otarídeos recentes apresenta uma plataforma secundária no sustentáculo bem desenvolvida (BERTA & DEMÉRÉ, 1986).

Os otarídeos são usualmente separados em leões-marinhos e lobos-marinhos, distinguíveis especialmente pelas características da pelagem: os lobos-marinhos são providos de uma capa exterior de pêlos cerdosos e bicoloridos, bem como de uma capa profunda de felpa, o que lhes confere a designação de lobos de dois pêlos ou "lobo peletero". Todavia, de forma geral, os lobos e leões-marinhos diferenciam-se também pelo menor tamanho e por um rostro mais afilado nos primeiros. REPENNING *et al.* (1971) descrevem que todos os lobos-marinhos possuem o terceiro incisivo superior com uma conspícua seção oval no nível basal do esmalte, ao passo que a maioria dos leões-marinhos tem uma seção transversal circular. Existem também diferenças comportamentais (BERTA & DEMÉRÉ, 1986).

Lobos e leões-marinhos são freqüentemente referidos como pertencentes a duas subfamílias: "Arctocephalinae" (Boeticher, 1934) (englobando *Callorhinus* e *Arctocephalus*) e Otariinae (Boeticher, 1934) englobando *Eumetopias*, *Neophoca* Peron, 1816, *Otaria*, *Phocartos* e *Zalophus* Lesson, 1828 (MITCHELL, 1968; TEDFORD, 1976; REPENNING & TEDFORD, 1977; RIEDMAN, 1990; REYNOLDS et al., 1999). Os "Arctocephalinae" são considerados mais ancestrais devido ao menor tamanho, pós-caninos multiradiculados (TEDFORD, 1976), menor desenvolvimento da camada de gordura, presença de dois tipos de pêlo e menor desenvolvimento do úmero (REPENNING & TEDFORD, 1977). Entretanto, a validade destas sub-famílias é questionada por inúmeros especialistas (*e. g.* MITCHELL, 1968; REPENNING *et al*., 1971; BARNES, 1989; BERTA & WYSS, 1994). As evidências contrárias à esta tradicional classificação advém do fato de que poucos caráteres diagnósticos efetivamente separam os dois grupos [*e. g.* pelagem e número de pós-caninos –sendo este último um caráter variável (KING, 1983). BRUNNER (2000), ao apresentar descrições anatômicas de todas as espécies de Otariidae, bem como BININDA-EMONDS *et al.* (1999), através de uma análise filogenética baseada em evidências morfológicas e paleontológicas não apóiam a validade das sub-famílias. BININDA-EMONDS *et al.* (1999) sugerem que dentre os leões-marinhos, o gênero *Arctocephalus* e o gênero *Callorhinus* formariam uma politomia. As subfamílias não são suportadas, tampouco, por dados moleculares e uma relação entre tais grupos também já foi sugerida com base no registro fóssil (MIYAZAKI et al. 1994).

De acordo com WYNEN *et al*. (2001), *Callorhinus ursinus* apresenta uma relação basal relativa a todos os demais membros da família, o que é coerente com o registro fóssil, sugerindo que este gênero divergiu há aproximadamente seis milhões de anos atrás. A classificação mais recente dos Otariidae baseia-se na morfologia craniana, dentição e distribuição geográfica (RICE, 1998). Outrossim, leões-marinhos e *Arctocephalus* irradiaram, aparentemente, muito rapidamente e o processo de tal radiação é mal compreendido até os dias de hoje (WYNEN *et al*. 2001).

Em um passado relativamente recente, a confusão quanto à taxonomia dos Otariidae era ainda mais acentuada dada a larga distribuição geográfica da família e a convergência de muitos caracteres

morfológicos entre alguns táxons (BERTA & DEMERÉ, 1986). Com efeito, apesar do notável aumento recente no conhecimento acerca de material osteológico e paleontológico, ainda há elementos da taxonomia corrente que carecem de estudos mais detalhados, como as relações taxonômicas entre as espécies da família, uma vez que mesmo híbridos intergenéricos são mencionados na literatura (BRUNNNER 2002; RICE 1998).

1.1.1.1. *Arctocephalus australis* (Prancha número 1)

Muitos foram os trabalhos que se dedicaram ao estudo e à descrição das espécies de *Arctocephalus* ("cabeça de urso": Gr.*arktos*=urso, Gr. *kephale*=cabeça) desde o Século XIX. *Arctocephalus australis* é muito menor que *Otaria* e costuma alimentar-se em áreas mais profundas, atingindo a borda da plataforma continental (BONNER, 1981).

Esta espécie reproduz-se em praias e ilhas e os grupos nas colônias são altamente variáveis, com as fêmeas esparsamente agrupadas[1]. O sistema de acasalamento de poliginia é moderado (aproximadamente cinco fêmeas/macho) e o dimorfismo sexual é pronunciado (RIEDMAN, 1990). Os machos atingem aproximadamente 189 centímetros de comprimento total de pesam entre 150-200 quilos quando adultos. As fëmeas medem cerca de 143 centímetros e pesam entre 30 e 60 quilos (WALKER, 1964).

REPENNING *et al.* (1971) apontam alguns caráteres no crânio das espécies de *Arctocephalus* que sugerem como a espécie ancestral *A. australis* (ou uma espécie semelhante a esta).

KING (1954) estabelece três subespécies para *Arctocephalus australis*, avaliando sobretudo variáveis morfométricas: *A. a. australis* para as populações das Ilhas Falklands (Malvinas), *A. a. gracilis* para as populações do continente e *A. a. galapagoensis* para as populações das Ilhas Galápagos, tendo sido posteriormente atribuído a esta última o *status* de espécie (*A. galapagoensis*) por REPENNING *et al.* (1971). Posteriormente, BONNER (1981) questiona a validade das subespécies *A. a. australis* e *A. a. gracilis*.

DREHMER (1994) apresenta um estudo anatômico detalhado do sincrânio e odontológico de *Arctocephalus australis*, ressaltando diferentes fases do desenvolvimento ontogenético (jovens e adultos) e dimorfismo sexual. Este autor destaca diversas estruturas anatômicas que "somente podem ser compreendidas através do desenvolvimento ontogenético, uma vez que a forma e os ossos que contribuem nas suas formações variam consideravelmente de acordo com o grau de maturidade do indivíduo" (op. cit: 157).

1.1.1. 2. *Callorhinus ursinus* (Linnaeus, 1758) (Prancha número 2)

O lobo marinho do norte distribui-se pelo Pacífico norte desde o mar de Bering até o sul da Califórnia (porção Leste de sua distribuição) e até o Japão Central ao oeste. Reproduzem-se em costas rochosas, apresentam fidelidade ao sítio e movimentos migratórios bem definidos.

A estação reprodutiva ocorre entre os meses de junho e julho e os picos de nascimentos ocorrem entre a segunda quinzena de junho e o início de julho. Já os picos no número de acasalamentos ocorrem a partir do final do mês junho (GENTRY & HOLT, 1986). As áreas reprodutivas normalmente situam-se sobre ilhas com grupos grandes e fêmeas densamente agrupadas[2]. O sistema de acasalamento é classificado como de poliginia extrema (aproximadamente 15-20 fêmeas/macho) e o dimorfismo sexual é considerado pronunciado (RIEDMAN, 1990).

[1]Este padrão pode alterar-se em função do meio ambiente (e. g. El Nino) e variando ainda conforme o sítio (e. g. se este está localizado na costa atlântica ou pacífica).
[2] Positivamente tigmotáteis e gregárias.

Os machos medem em média 2,1 metros e pesam entre 175-275 quilos ao passo que as fêmeas medem em torno de 1,4 m de comprimento e pesam entre 30 e 50 quilos. Diferencia-se das espécies de *Arctocephalus* especialmente quanto ao rostro, muito mais encurtado e de ângulo muito abrupto dorso-ventralmente (KING, 1983), além de peculiaridades nas nadadeiras anteriores e posteriores como o tamanho proporcional de tais membros (GENTRY, 1981).

Supõe-se que os dois gêneros evoluíram separadamente durante um tempo relativamente longo, pois *Callorhinus* é encontrado em águas subantárticas no Pacífico Norte (com exceção de um pequena população na Ilha de San Miguel, Califórnia) enquanto a grande maioria das espécies de *Arctocephalus* restringe-se ao hemisfério sul. Adicionalmente, *Callorhinus* parece ser mais pelágico do que as espécie de *Arctocephalus* (GENTRY, 1981).

1.1.1.3. *Otaria byronia* (Prancha número 3)

Otaria byronia é conhecida no Brasil como leão-marinho-do-sul, e se destaca por sua relativa abundância e ampla faixa de distribuição geográfica nas zonas costeiras da América do Sul (KING, 1983). O nome popular de *Otaria byronia* (leão-marinho) deve-se à proeminente juba presente nos machos adultos. De acordo com ROSAS (1989), os machos atingem maior tamanho e crescem mais rapidamente e por mais tempo do que as fêmeas. Os machos atingem aproximadamente 216-256 centímetros de comprimento total de pesam entre 200-350 quilos quando adultos. As fëmeas medem cerca de 180-200 centímetros e pesam entre 140 quilos (WALKER, 1964).

O nome da espécie para o gênero *Otaria* ainda está em discussão. Atualmente, tanto *O. flavescens* quanto *O. byronia* Blainville, 1820 estão em uso. RODRIGUEZ & BASTIDA (1993) revisaram toda a sinonímia, concluindo favoravelmente a *O. flavescens* considerando que (1) o espécime descrito como *Phoca byronia* também foi extraviado; (2) *O. flavescens* é o nome específico mais empregado entre os especialistas da América Latina e (3) o epíteto *flavescens* tem prioridade temporal. Entretanto, a Comissão Internacional de Nomenclatura Zoológica deliberou sobre a validade dos nomes favorável ao epíteto *byronia.* Uma vez que ambos os espécimes-tipo se perderam, é válido o nome que possui uma prova inequívoca da identidade do espécime[3], ainda que a localidade estivesse equivocada.

Otaria byronia Blainville, 1820 é a espécie de pinipédio mais comum no litoral-sul do Rio Grande do Sul (PINEDO, 1990) e a segunda mais freqüente nas praias mais ao norte do mesmo (SIMÕES-LOPES *et al*., 1995). Segundo PINEDO (1990), os indivíduos ocorrem principalmente entre o outono e a primavera.

Otaria byronia tem hábitos costeiros e oportunistas, sendo habitante de profundidades menores que 50 m (PINEDO, 1990). Ainda que essa espécie não seja considerada migratória, sabe-se que deslocamentos de machos são significativos (VAZ-FERREIRA, 1982).

Reproduz-se em praias arenosas ou rochosas e ainda em ilhas, e os grupos nas colônias apresentam um tamanho moderado a grande, estando as fêmeas densamente agrupadas. O grau de poliginia nesta espécie é classificado como moderado (5 a 15 fêmeas/macho) e dimorfismo sexual pronunciado[4] (RIEDMAN,1990).

Otaria byronia distingue-se dos demais leões-marinhos pelo palato secundário muito longo e de limite posterior muito côncavo (KING, 1954). BERTA & DEMÉRÉ (1986) apresentam um cladograma dos Otariidae onde aquela espécie é a mais derivada.

[3] No caso de *byronia*, esta prova trata-se de uma ilustração da vista palatal do crânio onde se observa a extensão de palato típica da espécie (prancha número 3).
[4] Os machos são pelo menos 50% maiores do que as fêmeas e normalmente estão presentes caracteres de dimorfismo secundário como, por exemplo, a presença da crista sagital no crânio.

1.2. HISTÓRICO

A partir dos anos setenta a teoria sintética passa a ser mais intensamente questionada, propulsionando a redescoberta da macroevolução, homologias, campos morfogenéticos e da heterocronia. Ressurge, por conseguinte, o interesse pelas investigações ontogenéticas como instrumentos elucidativos dos mecanismos evolutivos, bem como retornam ao centro do debate as implicações destas pesquisas para a sistemática biológica, sobretudo através de R. B. Goldschmidt em 1952 e C. H. Waddington em 1957 (FINK, 1982). A obra de S. J. Gould "*Ontogeny and Phylogeny*" publicada em 1977 também teve um papel essencial nesta tendência ao "exorcizar o fantasma de Haeckel" (1866), cuja base de dados original foi duramente questionada nas últimas décadas (RICHARDSON *et al.*, 1997). De acordo com Alberch (1982), o desenvolvimento não apenas é o agente através do qual as mudanças são promovidas, mas concomitantemente é também um fator limitante da habilidade da seleção de produzir novos fenótipos (ALBERCH, 1982).

Outrossim, este redirecionamento de enfoque parece sinalizar a emergência de uma nova síntese evolutiva, "mais robusta" (GILBERT *et al.,* 1996). Para tanto, foi fundamental a construção de propostas metodológicas que integrassem a dinâmica do desenvolvimento com a regulação gênica, ecologia e adaptação, pois a probabilidade de fixação de novas morfologias é determinada conjuntamente com parâmetros ecológicos, *e. g.,* tamanho populacional, estrutura reprodutiva (ALBERCH, 1982). 1.2.1. Ontogênese e a Diversidade Morfológica

1.2.1. Ontogënese e a Diversidade Morfológica

A despeito do aumento no número de análises moleculares que se referem à sistemática, grande parte das atividades mais rotineiras e fundamentais neste campo envolvem essencialmente decisões embasadas na variação morfológica.

O estudo da ontogenia é um tema central das ciências biológicas, uma vez que é a ontogenia que evolui e não os genes ou os indivíduos adultos (McKINNEY & GITTLEMAN, 1995).

EPSTEIN (1971) descreve que *Sus scrofa* Linnaeus, 1758 apresenta uma considerável mudança nas proporções cranianas ao longo do crescimento. Segundo tal autor, estas modificações na forma no decorrer da ontogênese se dão paralelamente a uma considerável diversidade craniana entre adultos das diferentes raças e muitas destas possuem proporções claramente juvenilizadas no crânio.

Segundo RADINSKI (1984), as modificações alométricas têm um papel de destaque em suas inferências sobre a evolução do crânio. Este autor conclui que algumas variáveis crescem com expoentes similares aos observados nas séries filogenéticas, enquanto outros crescem com expoentes significativamente mais baixos.

WAYNE (1986) estudou a influência do desenvolvimento nas modificações morfológicas em canídeos. Aquele autor emprega dados do crescimento de *Canis familiaris* Linnaeus, 1758 para investigar os mecanismos de desenvolvimento que originaram diferentes raças. Ele constatou uma certa constância no crescimento dos componentes do crânio entre os canídeos ao longo da ontogenia. Tal autor sugere que esta similaridade (que transcende diferentes níveis taxonômicos entre as variedades de cão doméstico e das espécies de canídeos selvagens) pode refletir pressões de seleção similares, ausência de variação no desenvolvimento ou ambas.

DREHMER & FERIGOLO (1997) comparam o sincrânio de *A. australis* com o de *A. tropicalis*. Estes autores constataram crescimento alométrico no rostro e na órbita destas espécies e sugerem que tal alometria seria "...a expressão de processos heterocrônicos atuando na evolução destas espécies e em

última análise na evolução dos otarídeos em geral " (p.: 149).

SANFELICE (1999) apresentou uma comparação entre os sincrânios de adultos de *Otaria byronia* e *Arctocephalus australis*, onde refere evidências da atuação de processos heterocrônicos sobre tais espécies, grande variabilidade anatômica e a necessidade de estudos ontogenéticos para o entendimento do fechamento sutural (e por conseguinte do crescimento craniano), das relações e origem de determinados acidentes anatômicos, bem como da anatomia dentária, sobretudo no que se refere à anatomia radicular.

WOODBURNE & MACFADDEN (1982) ressaltaram a importância da alometria na ontogenia para a evolução morfológica em cavalos. Estes autores demonstram relações entre aumento no tamanho, maturidade relativa e modificações nas proporções ao longo da evolução dos cavalos.

THOROGOOD (1988) analisou o desenvolvimento do crânio em geral. Ele colocou as diferenças filogenéticas na forma do condrocrânio como consequências do crescimento alométrico, de alterações heterocrônicas na taxa e no tempo dos eventos no desenvolvimento e de adaptações funcionais ocasionais relacionadas ao ambiente.

Processos e tendências evolutivas podem ser melhor compreendidos através de uma investigação da ontogenia. Sabe-se que estudos sobre crescimento permitem investigar os caminhos evolutivos de um organismo e as maneiras como estas trajetórias são modificadas, uma vez que as mudanças no padrão de desenvolvimento conduzem a modifidações filogenéticas na morfologia do adulto (FIORELLO & GERMAN, 1997).

1.2.2. Relevância do Desenvolvimento para os Estudos Evolutivos:

Comumente mudanças no tempo de desenvolvimento são mencionadas como uma fonte primária para a evolução morfológica por ser uma fonte de variação herdável sobre a qual a seleção atua (FIORELLO & GERMAN, 1997). Mais ainda, atualmente verifica-se uma tendência mundial que enfoca o estudo da ontogenia como uma fonte de compreensão dos mecanismos da mudança evolutiva, bem como da eficiência fisiológica e ecológica de mudanças nas faixas de proporções possíveis. Deste modo, o estudo da ontogênese ultrapassa largamente os limites puramente descritivos (GOULD, 1966; 1977).

Dentro disto, a heterocronia tem se colocado no centro do debate que surgiu a partir da lei biogenética de HAECKEL (1886) ("a ontogenia recapitula a filogenia") e da afirmação de DE BEER ("Phylogeny is due to modified ontogeny"; 1930), debate este que vem se intensificando nas últimas décadas (e. g. GOULD, 1977; McKINNEY, 1988; LONG, 1990; McKINNEY & McNAMARA, 1991). Nesta polêmica destacam-se questões que abordam a natureza da relação entre o desenvolvimento individual e a história filogenética, a existência de uma relação de "causa", como esta relação operaria e qual a sua relevância na evolução.

Neste contexto, cabe aqui abordar brevemente a relação entre a heterocronia e a ontogenia. A heterocronia pode ser definida como "changes in relative time of appearance and rate of development of characters already present in ancestors" (GOULD, 1977:2). Ora, mudanças no tempo de desenvolvimento ocorrem também entre gerações dentro de uma mesma espécie como parte da variação fenotípica. Quando os caráteres morfológicos devidos/relacionados à tais mudanças possuem significado adaptativo, pode ocorrer uma seleção preferencial pelo morfótipo derivado, tendo como conseqüência a especiação (McNAMARA, 1986). Isto está relacionado ao fato de que o tempo dos eventos ao longo do desenvolvimento pode também afetar as relações nos caráteres do adulto e responder à seleção (RISKA, 1986).

SHEA (1988) afirmou que apenas estudos ontogenéticos e heterocrônicos podem determinar se uma intensa diferenciação na forma não está intimamente relacionada a uma seleção sobre o tamanho, em contextos ecológicos particulares. Através de exemplos oriundos de estudos morfológicos em primatas, aquele autor considera essenciais estudos ontogenéticos comparativos (sob uma perspectiva heterocrônica) para a elucidação de aspectos da biologia funcional e da adaptação de regiões específicas do corpo. Além disto, também a análise do dimorfismo sexual sob a perspectiva da ontogenia é, segundo SHEA (1988), necessária na maioria dos grupos de mamíferos, e uma das áreas de maior importância para a aplicação da heterocronia em um futuro próximo. Por fim, o autor ressalta a relevância central de pesquisas adicionais na covariação dos padrões de tamanho e forma com relação à idade para o entendimento dos processos heterocrônicos.

Contudo, cabe aqui considerar ainda que a heterocronia mantém-se ainda nos dias de hoje em um cenário disputado, sobretudo no que concerne ao método para a sua investigação e também a questões nomenclaturais. Dentro disto, outros padrões de resultados relativos ao desenvolvimento vêm sendo retomados ou apresentados na literatura mais recente, como é o caso da Heterotopia.

Este termo foi cunhado por HAECKEL no início do século em 1866 e tem ressurgido na literatura mais recente como uma alternativa para a compreensão dos padrões ontogenéticos vinculados à mudanças evolutivas (ZELDITCH, 2001). Outros padrões tais como a heterotipia e a heterometria aparentemente também vem ganhando espaço paralelamente ao refinamento e redefinição das técnicas analíticas.

1.2.3. Desenvolvimento, Alometria e Evolução

Estudos de cunho heterocrônico estão às vezes associados a estudos de alometria. Outrossim, o estudo do tamanho e suas conseqüências para o desenvolvimento e a evolução estão bem apresentados no clássico trabalho de STEPHEN JAY GOULD "*Allometry and size in ontogeny and phylogeny*" (1966). De acordo com aquele autor, o estudo da dependência do tamanho na forma e na função é de grande relevância na busca de uma teoria geral da forma que reflita a diversidade.

Contudo, e à semelhança das mudanças no tempo e nas taxas de desenvolvimento, a alometria relaciona-se com modificações evolutivas na forma ao longo das ontogenias, mas os padrões alométricos não podem ser usados para inferir processos heterocrônicos (podendo sim ser o resultado de um destes últimos). Ora, a heterocronia versa sobre mudanças evolutivas na forma através de modificações nas taxas e no tempo dos processos ontogênicos e reporta-se à idade. A alometria por sua vez caracteriza padrões de variação de traços e reporta-se ao espaço ocupado pelo caracter, de tal sorte que são mecanismos distintos e complementares (KLINGENBERG & SPENCE, 1993).

Os métodos empregados estão "progredindo" a passos largos, tanto no que concerne aos procedimentos experimentais quanto aos aspectos matemáticos (*e. g.,* BOOKSTEIN, 1998). O mesmo é válido para as discussões a respeito das limitações das hipóteses de especiação alometricamente embasadas. A solução deste dilema/impasse recorrente pode ser encontrada atualmente através da análise do tipo de conjunto de dados, das conclusões cabíveis, e da viabilidade das técnicas analíticas multivariadas ou de deformações (*e. g.,* BOOKSTEIN, 1976; 1978, SWEET, 1980).

Freqüentemente associada no século XIX com o ideário ortogenético, a abordagem da alometria relacionada ao par ontogenia/filogenia iniciou com HUXLEY (1924; 1932) e TESSIER (1931) e foi continuado através dos estudos das taxas de crescimento alométricos geneticamente controladas ou fixadas (COCK, 1966; DAVIS, 1962). Segundo RENSCH (1954), a alometria reflete os resultados da

seleção natural direta (seleção sobre taxas que geram alterações adaptativas) ou indiretamente. De fato, os princípios comumente empregados nos estudos da alometria ontogenética mantinham um certo caráter abstrato até a metade do século XX, contrastando com os avanços no campo dos mecanismos endocrinológicos, de organogênese e fisiológicos (BONNER, 1952). No entanto, este cenário alterou-se com a sofisticação das técnicas analíticas, como mencionado no parágrafo anterior.

1.3. JUSTIFICATIVAS

Uma vez que a ontogenia pode ser o determinante comum para padrões alométricos refletidos nos adultos, estudos referentes ao desenvolvimento são muito relevantes para ampliar a compreensão de aspectos da evolução dos pinipédios, como por exemplo a variação, a diversidade específica e o dimorfismo sexual. Além disto, o crânio (objeto de estudo do presente trabalho) possui valor singular dentre os vertebrados por configurar-se em um clássico indicador das relações de parentesco dadas sua estrutura e integração (ZELLER, 1986).

Outrossim, ainda que as relações e a sistemática dos Pinnipedia (bem como da ordem Carnivora se configurem em uma temática controversa desde o século XIX, poucos são os estudos sobre a morfogênese das espécies que compõem este grupo. Com efeito, o crânio é sempre privilegiado no contexto das investigações taxonômicas dado sua constância e riqueza de caráteres. Entretanto, quando se quer compreender efetivamente os componentes individuais deste e como tais estruturas formam esta estrutura única, faz-se necessário uma análise detalhada de toda a ontogenia e suas múltiplas fases.

Conforme ressaltado anteriormente, a ontogenia é, literalmente, um estoque de morfologias onde pequenas mudanças no tempo de desenvolvimento ou alterações genótipicas podem atuar, alterando-as em dimensões diversas (GOULD, 1977).

1.4. OBJETIVOS

(1) Desenvolver um estudo comparado do dimorfismo sexual e da disparidade da forma nas espécies aqui enfocadas;

(2) Avaliar a importância da alometria para o desenvolvimento morfológico;

(3) Testar a operação dos padrões de mudanças da ontogenia *(e. g.,* heterocronia, heterotopia, re-estruturação do padrão alométrico), descrevendo e discutindo seus efeitos em cada grupo enfocado;

(4) Identificar modificações na morfogênese (compartilhadas ou não entre os grupos) com vistas a edificar inferências sobre a ontogenia e sua rela;áo com os padrões de histórias-de-vida das espécies;

(5) Dar a conhecer os padrões de crescimento e desenvolvimento de Otariidae;

(6) Comparar e avaliar a efetividade dos métodos de morfometria tradicional e geométrica para a concretização dos objetivos supramencionados.

2 MATERIAL E MÉTODOS

Podemos dizer que nos últimos anos as técnicas de morfometria passaram por uma verdadeira revolução desde o trabalho seminal de BOOKSTEIN (1991). O advindo da morfometria geométrica mudou de maneira bastante radical o método de análises das formas biológicas. Este fato é de suma importância, uma vez que a forma dos organismos e das estruturas biológicas é um dos principais alvos das ciências naturais por evidenciar os aspectos mais conspícuos do fenótipo e por representar o elo entre o genótipo e meio ambiente (MONTEIRO *et al.,* 2002).

A premissa básica da morfometria geométrica refere-se à aquisição e quantificação da forma empregando coordenadas cartesianas de marcos anatômicos geometricamente homólogos. Destacam-se como ferramentas de análise da forma a sobreposição de Procrustes e as deformações parciais e relativas. Todavia, o ponto central e mais vantajoso desta abordagem refere-se à separação entre a forma geométrica e o efeito de escala. Ao transformar uma configuração de marcos anatômicos através dos processos de translação, rotação e proporcionaliza;áo, toda a informação referente ao efeito de escala é removida, sem no entanto retirar a informação que concerne à covariação da forma com o tamanho[5].

2.1. MATERIAL EXAMINADO

O material utilizado neste estudo compõe uma amostra transversal de crânios de *Arctocephalus australis* (n=153), *Callorhinus ursinus* (n=55) e *Otaria byronia* (n=295). Apenas a amostra desta última espécie continha espécimes de diferentes regiões geográficas. Deste modo, esta amostra foi dividida entre espécimes procedentes de **(a) Rio Grande do Sul ou Uruguai ou Buenos Aires**; e espécimes procedentes de **(b) Patagônia argentina**. Estas sub-amostras foram comparadas através de duas metodologias:

(a) Comparação das médias de cada medida linear através de um teste T bi-modal (as variâncias foram testadas quanto a sua homogeneidade anteriormente).

(b) Comparação das formas médias de cada amostra através de um teste não-paramétrico, similar ao teste F. O método da aleatorização foi utilizado para estabelecer intevalos de confiança e determinar a significância da diferença entre as distâncias parciais de Procrustes entre as sub-amostras.

Este material[6] encontra-se depositado nas coleções científicas das instituições abaixo relacionadas.

(1) Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul;

(2) Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul;

(3) Laboratório de Mamíferos Aquáticos da Universidade Federal de Santa Catarina;

(4) Facultad de Ciencias de la Universidad de la República, Montevideo, Uruguai;

(5) Centro Nacional Patagônico, Puerto Madryn, Chubut, Argentina;

(6) Museu Argentino de Ciências Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina;

(7) Museum of Vertebrate Zoology, University of California, Berkeley – Califórnia/EUA;

(8) California Academic of Science, San Francisco – Califórnia/EUA;

(9) University of Michigan, Museum of Zoology, Ann Arbor – Michigan/EUA

[5] Isto ocorre porque, quando da presença de alometria as coordenadas irão variar conforme o tamanho do centróide.
[6] Totalidade do conjunto das 3 espécies amostradas.

2.2. Determinação da faixa etária e da idade absoluta

Foram analisados neonatos, jovens, subadultos e adultos de ambos os sexos das três espécies enfocadas. Trataram-se como neonatos os filhotes coletados até três meses de idade, aproximadamente. Jovens, subadultos e adultos foram definidos de acordo com o método de SIVERTSEN (1954) com base nas suturas cranianas, concomitantemente com o método de HAMILTON (1934) e PAYNE (1979) para a determinação da idade a partir das camadas de deposição de dentina/cemento nos dentes.

Os caninos (preferencialmente os superiores) foram bi-seccionados longitudinalmente com serra circular diamantada, polidos com lixas d´água de diferentes granulometrias (400, 500, 1000 e 2000) e descalcificados em uma solução de ácido fórmico a 5%. Na seqüência, as secções foram lavadas em água corrente e secas à temperatura ambiente. Após, foram observadas em microscópio estereoscópio para contagem das camadas, seguindo LAWS (1962).

2.3. Medidas lineares

As medidas craniométricas foram tomadas ao milímetro mais próximo com paquímetro de precisão (*Mitutoyo* ou *Starret*; 500 cm). As medidas adotadas seguem HUE (1907), COMMITTEE ON MARINE MAMMALS (1967), BURNS *et al.* (1984), FEDOSEEV (1984), XIMÉNEZ *et al*. (1984), WIIG & LIE (1984), KERLEY & ROBINSON (1987), WYSS (1987) e DREHMER & FERIGOLO (1996, 1997). Em caso de bilateralidade, o lado esquerdo foi medido.

2.4. Registro Fotográfico

Para o registro e estudo fotográfico foram utilizadas as câmeras *Minolta* STR 101 ou *Pratika*, lentes normal (50 mm) e macro (70-210 mm), além de uma câmera digital *Nikon Coolpix* 950 35 mm, sob luz natural ou refletida e com tempo de exposição e aberturas variáveis. As imagens foram salvas no formato "*Joint Photographic Experts Group, *.JPG*" e editadas no *Corel Photoshop*. Os filmes fotográficos (quando estes se fizeram necessários) empregados foram Plus-X (Kodak) ISO 125 ou FUJI Féria ISO 400.

Previamente ao registro fotográfico, foi colocado um papel quadriculado no campo fotográfico a fim de controlar o efeito “arco-íris” e determinar a extensão da região de distorção de modo a posicionar a câmera corretamente (a uma distância que foque os espécimes fora desta região). Outrossim, a profundidade de campo foi checada em conformidade com o tamanho dos espécimes.

2.5. Terminologia básica inerente às técnicas de Morfometria Geométrica para análise da forma

Os conceitos apresentados abaixo seguem essencialmente MARCUS *et al.* (1986), MONTEIRO *et al.* (2002) e ZELDITCH *et al.* (in press).

Marcos Anatômicos (landmarks) - Pontos anatômicos discretos que podem ser reconhecidos como os mesmos pontos (pontos homólogos) em todos os espécimes estudados.

Variável de forma (shape variable) - Qualquer medida em uma configuração de marcos anatômicos que não modifica seu valor quando todos os comprimentos são multiplicados por um fator escalar *x* (BOOKSTEIN, 1991).

Centróide (centroid)– Ponto médio da configuração, também chamado “centro de massa. O tamanho do centróide é calculado como a raiz quadrada da soma das distâncias quadradas entre cada marco anatômico e o centróide da forma.

Linha de Base (baseline) - Linha que se estende entre dois marcos anatômicos fixos a qual será a referência para a sobreposição dos marcos quando da construção de coordenadas de forma (Bookstein Shape Coordinates).

Espaço da figura (figure space) - De dimensão igual ao número de pontos da configuração (*p*) multiplicado pelo número de dimensões em que os dados forma coletados (*k*) (dois, no caso de figuras planas).

Espaço de "pré-form" (pre-form space) – Espaço formado pelas coordenadas quando configurações são transladadas para uma mesma posição no espaço, de modo que os centróides fiquem superpostos. Sua dimensionalidade é *pk-k*. Isto acontece porque as coordenadas do centróide estão fixas em todos os objetos (MONTEIRO & REIS, 1999).

Espaço de "form" (form space) - Quando as configurações são transladadas e rotacionadas em concordância com um dado critério de otimização, mas não foram proprocionalizadas. Este espaço apresenta dimensionalidade igual a *pk-k-k (k-1)/2*. Em duas dimensões, um ângulo de rotação é fixo (e as k coordenadas do centróide também estão fixas).

Espaço de pré-forma (pré-shape space) - Espaço descrito pelas coordenadas quando as configurações são transladadas e proporcionalizadas (centradas e com tamanho de centróide igual a unidade). Logo, formas que diferem apenas quanto à rotação posicionam-se sobre um arco circular, o que se define por/como "*fibra*". Sua dimensionalidade é representada por pk-k-1 e corresponde a uma série de fibras. Estas fibras aproximam-se e afastam-se em conformidade com a orientação em que se encontra a configuração de pontos.

Espaço de forma de Kendall (Kendall space of shape)- Neste espaço, as configurações estão centradas em um local comum, proporcionalizadas quanto ao tamanho rotacionadas segundo um critério de otimização que minimiza a soma dos quadrados das distâncias entre pontos homólogos num par de configurações. A dimensionalidade desse espaço é pk-k-k(k-1). A superfície é definida na posição em que as fibras do espaço de pré-forma estão à menor distância possível umas das outras. Sabe-se que cada ponto no espaço de forma corresponde a uma fibra no espaço de pré-forma.

Distância de Procrustes (Procrustes Distance) - É a distância que constitui a métrica do espaço de forma de Kendall, sendo assim medida no espaço curvo e tendo seu tamanho livre para variar. Mais especificamente, esta distância é a mínima soma dos quadrados das distâncias entre pontos homólogos num par de configurações após a aplicação do processo de sobreposição. Com efeito, seu valor é uma soma de quadrados que pode ser dividido pelo número de graus de liberdade apropriado e transformado em quadrado médio. (Variância). Por conseguinte, as distâncias de Procrustes podem ser empregadas em vários delineamentos experimentais baseados em modelos de análise de variância e substituir valores de soma de quadrados e quadrados médios em análises estatísticas multivariadas que se baseiam no modelo linear geral, como a regressão multivariada (MONTEIRO & REIS, 1999).

Todavia, a métrica de Procrustes determina que o espaço de forma é não-Euclidiano. Por conseqüência, convém que os espécimes (que estão no espaço de forma) sejam analisados através de sua projeção em um espaço tangente, com a mesma dimensionalidade e onde as distâncias entre indivíduos espaço tangente aproximam-se bastante das distâncias não-lineares no espaço de forma. Assim, nenhuma informação relevante é perdida (MONTEIRO & REIS, 1999).

Espaço tangente (tangent space)- É muito mais prático e simples comparar formas em um espaço linear, cujas propriedades matemáticas foram exploradas em maior detalhe, especialmente quando

tratam-se de sistemas biológicos. Assim, o espaço curvo é substituído por um plano próximo a esta distância entre as formas. Mas é importante que a região ocupado pelas formas na superfície curva seja relativamente pequena[7].

Entretanto, existem dois tipos de espaços tangentes: aquele tangente ao centro do espaço da pré-forma (onde as distâncias são denominadas *Distâncias de Procrustes Parciais* e a sobreposição que a minimiza é denominada *Sobreposição de Procrustes* e aquele tangente ao espaço de forma. A *Distância de Procrustes Parcial* possui o tamanho do centróide fixado no valor da unidade ao passo de que na *Distância de Procrustes* (distância linear medida no espaço tangente ao espaço de forma) apenas a configuração de referência tem o centróide estandarizado e fixo no valor da unidade. As demais podem variar o *tamanho do centróide* conforme o coseno de "p".

Forma de Referência (reference shape) - Aqui, a premência está em discutir os critérios de escolha da forma de referência, mais do que defini-la (sua definição, relacionada diretamente com sua função no desenrolar das análises, pode ser facilmente intuída).

Para tanto, é preciso ter em conta que a diferença entre a aproximação do espaço euclidiano (plano tangencial) e a Distância de Procrustes aumenta geometricamente, o que pode separar excessiva e problematicamente a referência das formas enfocadas. Para minimizar este efeito indesejado na amostra com um todo, utiliza-se a média desta como a forma de referência.

Por outro lado, casos em que organismos são tão grotescamente distintos em forma (ao ponto de que a aproximação pelo espaço tangente não se configure em uma aproximação válida) são raríssimos. Sendo assim, a escolha da forma de referência não é um tema crucial, e muitos autores escolhem a referência conforme as hipóteses biológicas sob investigação (ZELDITCH *et al.*, 1995). Entretanto, estes sofrem a objeção de que a aproximação do espaço tangente não se tornaria válida nestas condições (ROHLF, 1998). Com efeito, usar a forma média de todos os espécimes minimiza a possiblidade de que a distância euclidiana não represente adequadamente a Distância de Procrustes.

Neste contexto, optou-se por utilizar a forma média da amostra como forma de referência nas análises estatísticas. O ponto inicial (como a forma média na idade zero ou a forma estimada no tempo=0) foi usado como referência para elaborar as ilustrações.

A função "thin-plate spline" - Modela o comportamento de uma placa[8] quando é deformada para ajustar-se a uma configuração de marcos que está sob esta placa, uma configuração abaixo da placa (BOOKSTEIN, 1989b). Imagina-se que sobre esta placa estão fixados os marcos anatômicos de uma configuração. Sob a placa está uma configuração que correspondente à configuração-alvo (na qual intentemos transformar a configuração que está sobre a placa). O processo de transformação da configuração tangente para que os marcos de uma estejam superpostos aos da configuração sob a placa, implica numa deformação da placa. Este processo implica em gasto de energia (exceto para as transformações uniformes, que envolvem somente movimentos de inclinação e mudanças de direção da placa, portanto apresentam energias de deformação iguais a zero). E como em uma placa real, a energia necessária para deformar um grupo de marcos anatômicos depende da distância que estes se encontram uns dos outros: quanto mais próximos os marcos, mais energia é necessária para a deformação da placa.

[7] É importante que a região ocupada pelas formas na superfície curva seja pequena para minimizar as distorções. O princípio aqui é o mesmo das projeções cartográficas

[8] de proporções lineares e infinitamente fina

A matriz da energia de deformação é definida pela geometria da configuração de referência[9]. A partir da matriz de energia de deformação podemos construir um subespaço localizado tangente ao espaço de forma na vizinhança da configuração de referência. Isto faz com que a escolha mais lógica da referência seja uma configuração média da amostra calculada pela sobreposição ortogonal pelos quadrados mínimos.

As deformações parciais são componentes geometricamente ortogonais da deformação modelada pelo "*thin-plate spline*". A deformação é decomposta em dois componentes: o *uniforme* e o *não-uniforme*. O componente uniforme descreve mudanças na forma que são geometricamente uniformes ao longo de todo o objeto de estudo. O *componente não-uniforme* compõem-se de uma série de dimensões progressivamente mais e mais localizadas (as deformações parciais).

Tipos de sobreposição utilizados - É possível utilizar um tipo de sobreposição para as análises estatísticas e outro para as representações gráficas sem qualquer inconsistência entre as inferências estáticas e as deduções biológicas pois estas não dependem da escolha das variáveis (*e. g.,* deformações parciais ou coordenadas de forma). Para uma revisão dos métodos de sobreposição[10], veja ZELDITCH *et al.* (in press).

Coordenadas de Forma de Bookstein (Bookstein shape coordinates) - Nesta superposição, a configuração de marcos é transformada de forma que dois marcos sejam coordenadas iguais a (0, 0) e (1, 0). Estes marcos constituem a chamada *linha de base.* Uma das principais vantagens deste método é que, como dois pontos da configuração estão fixos, a descrição dos deslocamentos relativos dos demais marcos anatômicos é facilitada. Outrossim, este método preserva os graus de liberdade adequados aos testes análiticos. Todavia, a variância dos marcos fixados na linha de base é transferido para outros pontos. Este "ruído" é agravado pelo fato de que a variância transferida está relacionada à distância dos demais marcos anatômicos até a linha de base, o que potencialmente pode induzir a correlações entre os marcos anatômicos. Adicionalmente, a soma dos tamanhos dos vetores de cada marco anatômico[11] não corresponde à soma do total das distâncias entre as formas (em conseqüência, não representam a total magnitude da diferença) e o escalonamento não é consistente com a métrica de Procrustes (as formas são escalonadas de acordo com a linha de base – comprimento da linha de base = 1) e não com o tamanho do centróide unitário, como estipulado na teoria da Morfometria Geométrica vigente.

Sobreposição Ortogonal pelos Quadrados Mínimos (general least square sobreposition) - O ajuste é feito pela sobreposição de cada espécime da amostra a uma configuração média de modo que a soma dos quadrados das distâncias entre os pontos correspondentes, em ambas as configurações, seja a menor possível. Para tanto, realizam-se as operações de translação, rotação e "proporcionalização" das formas.

Aqui, o tamanho imperativamente define-se em termos do centróide da configuração. A utilização do tamanho do centróide como variável de tamanho padrão em todas as análises geométricas, em detrimento de outras variáveis é justificada pelo fato de o tamanho do centróide ser a única variável de tamanho que não se correlaciona com a forma, quando o modelo nulo da alometria é verdadeiro (BOOKSTEIN, 1991).

[9] O nome "energia de deformação" refere-se à energia necessária para deformar uma certa região da placa de metal e não à energia utilizada para transformar a referência numa configuração alvo.
[10] Para uma revisão e discussão dos tipos de sobreposição, ver ZELDITCH et al. *in press*.
[11] Que representam as diferenças entre as formas

Este método de sobreposição apresenta algumas vantagens sobre o método das coordenadas de forma: é consistente com a métrica de Procrustes no que concerne a dissimilaridade entre as formas e a variância dos pontos fixados na linha de base não é transferida (pois não há marcos impedidos de variar). Contudo, apresenta o dobro de coordenadas do que marcos anatômicos (dificultando o emprego de testes estatísticos analíticos). Em acréscimo, o método rotaciona as formas livremente para maximizar a similaridade, ainda quando tais rotações não correspondem a possibilidades biológicas viáveis.

CAPÍTULO I

THE LINEAR MEASUREMENT APPROACH AND THE ONTOGENY OF SEXUAL DIMORPHISM IN OTARIDS: A COMPARATIVE ANALYSIS AMONG *Arctocephalus australis, Callorhinus ursinus* AND *Otaria byronia* (PINNIPEDIA: MAMMALIA)

THE LINEAR MEASUREMENT APPROACH AND THE ONTOGENY OF SEXUAL DIMORPHISM IN OTARIDS: A COMPARATIVED ANALYSIS AMONG *Arctocephalus australis, Callorhinus ursinus* AND *Otaria byronia* (PINNIPEDIA: MAMMALIA)

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ABSTRACT

Adult phenotypes arise through ontogeny. Changes in ontogeny within an evolving lineage therefore ought to produce changes in phenotype. Skull´s trajectories of *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia* are characterized using PCA analysis and then compared through calculations of the angles between allometry vectors. Individual coefficients of vectors are compared after calculation of bootstrapped confidence intervals. Our aims are to analyse the conservation of ontogenetic trajectories over time, between sexes and between species; to characterize growth trajectories and, finally, to compare them among taxa with respect to isometry. The allometry vectors for all species were significantly different from isometry. Dimorphism in the allometric vector are observed only in *O. bryonia* and the difference between males and females of the fur seals are related with adult body size. The comparisons species/sex groups revealed similar vectors (any significant shape disassociation are verified in the inter-specific analyzes), suggesting lower plasticity of the ontogenies.

INTRODUCTION

The inherent difficulties in deriving general principles of morphogenesis are reflected in the levels of abstraction (e. g. “growth gradients”, “morphogenetic fields”) in studies of ontogenetic allometry (BOONER, 1952). This is also reflected yet in the multiplicity of terms associated with the interrelation of growth processes in ontogeny and the modification of form in phylogeny (e. g. DE BEER, 1940), even after the provision of general models by GOULD (1977) and ALBERCH et al. (1979).

However, we can say that allometric responses seems to be the rule (not the exception), in ontogeny and phylogeny, and HUXLEY (1924) and TESSIER (1931) strongly impulsed the allometric investigations in ontogeny and phylogeny. Some year after that, these studies were incorporated into the framework of the Synthetic Theory (ALBERCH, 1980).

Actually, the progress in the comparative and phyletic branches of allometric investigation is notable due to the infusion of formal analytic methods and an increased level of sophistication over the techniques of D´Arcy Thompson that improves consistency to the analysis and approaches (ALBERCH, 1980). Allometry is an integral part of heterochronic analysis and does provide useful ontogenetic information even without age data.

Analyses of Principal Components, for example, are useful for the interpretation of components via group ordination and to measure the multivariate variation in the calculation of ontogenetic trajectories (KLINGENBERG, 1993).The relationship between *x* and *y* often follow the power law of HUXLEY (1932) and it is usual that the coefficients are estimated by simple or multivariate bivariate regression (ZELDITCH et al. *in press*). The interpretation of the allometric coefficient *k* is easy and it represents the growth rate of one measurement relative to that of a standard: that is the growth rate of the dependent variable. Nevertheless, the biological meaning of the intercept is less straightforward because its value depends on the units of measurement and especially because, sometimes, when log(*x*) =0, *y* might not even exist[12]. On the other

[12] Extrapolation behind that point is valid only for the range of sizes over which the model fits the data, which might not be the whole of ontogeny (ZELDITCH et al., *in press*).

side, it is not possible estimate correctly *y* without *b* and when groups do not differ in *k*, a difference in *b* suggest a distinct proportions at the outset of growth that persists throughout all of growth (ZELDITCH et al., *in press*). Most of the theoretical literature has focused on *k* from both spatial and temporal[13] perspectives) because *b* is static. This becomes evident when considering why the power law holds in the first place. As mentioned before, the primary biological explanation for allometry is that growth is a multiplicative process. When analyzing the relationship between size and time, the best-fitting models are usually not linear but rather sigmoidal in form. But equally common is the use of the Principal Components Analysis (PCA) since JOLICOEUR (1963) proposed that PC1 commonly is a multivariate allometry vector when it is extracted from a variance-covariance matrix of log-transformed measurements. The mechanical principals support the view that allometry is an important component of intraspecific variation and can be a determinant of the direction of evolutionary change and an important constraint of evolutionary changes in shape; a view which has had a profound influence on the development of evolutionary theory (McNAMARA, 1986).

On the other hand, the empirical evidence that allometry accounts for sufficient shape variation to be an effective constraint is not proportional because most of the studies confound size and shape (SWIDERSKI, 1993). Commonly, the analyzed distances are a subset of some distances among points where many measurements redundantly evaluate the same anatomical feature/direction while others are under sampled or completely omitted (STRAUSS & BOOKSTEIN 1982). Consequently, the high correlations observed in many analyses are partly due to the redundancy of the measurements considered or yet to the omission of data from independently varying regions (SWIDERSKI, 1993).

Of course, bias in selection of measurements can be minimized, but this does not solve the problem that partitioning the variances of a set of distances does not produce independent size and shape variables (BOOKSTEIN, 1989). Thus, it is impossible to know whether an allometric vector represents a large proportion of the shape variation or just a large proportion of the size variation.

But with more consistent information about the spatial determination of morphogenesis, in conjunction with that on its temporal organization, we can establish relationships between the allometric coefficients to the underlying developmental processes that explain them. Otherwise, considering that the theories of developmental controls over the spatiotemporal organization of morphogenesis may be most easily expressed in terms of linear morphometric measurements, studies of allometry using this kind of datasets are an important part of evolutionary developmental biology. Allometric coefficients are also undoubtedly informative about the relationship between form and function and the literature on biomechanics is filled with theories that predict scaling relationships among measurements. Applied to ontogenetic series, such theories may explain ontogenetic allometry in terms of the ontogeny of function. In that controverse context, we aim to compare the allometric patterns of *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia* taking in account the ontogenetical stages and the sexual dimorphism of the otarids. We also intent to test for channeling (to verify conservation or variability of ontogenetic trajectories over time). So, we can say that a major aim is to quantify each growth trajectory and discover whether the variables constituting each trajectory change in concert over phylogeny.

[13] Even though time is not explicitly incorporated in studies of allometry, it is nonetheless implicit (LAIRD et al; 1968)

MATERIAL AND METHODS

This study is based on a sample of three species of otarids, comprising males and females spanning all age periods from infant to the mature adult stage[14].

Table 1. Description of the sample size for each studied species separated by sex.

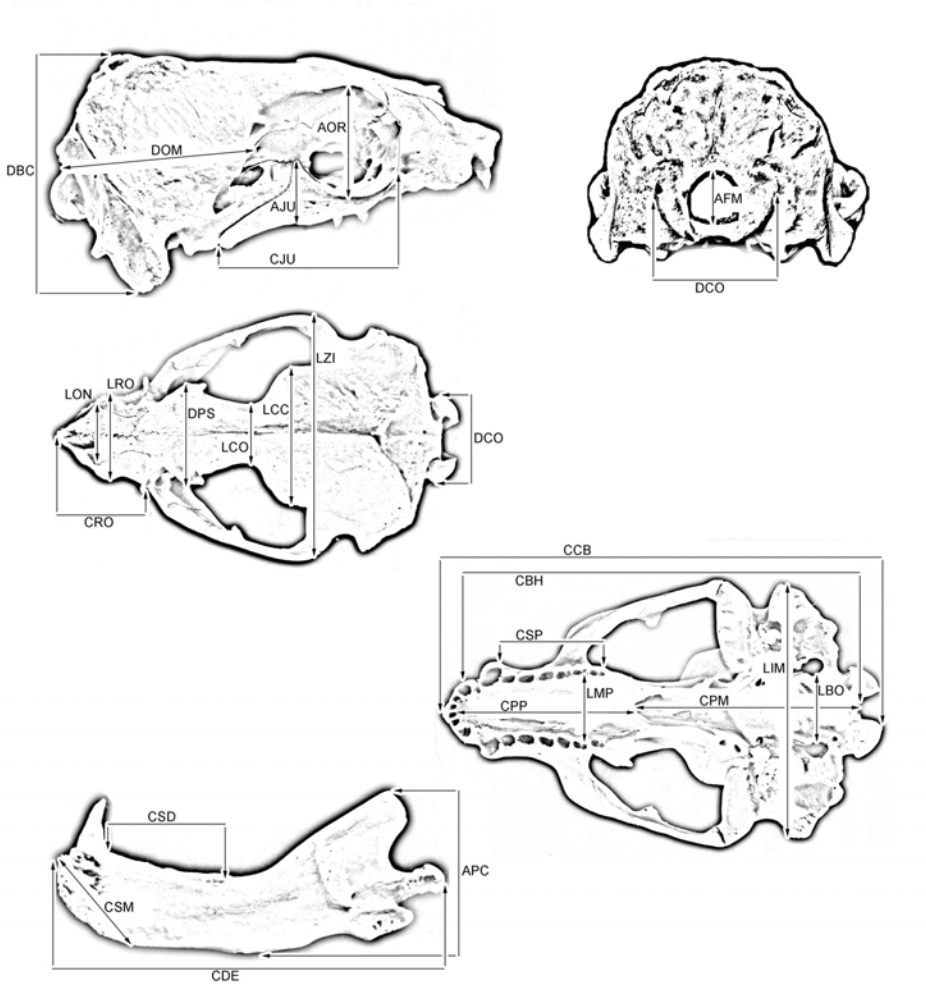
	FEMALES	RANGE OF TOTAL LENGTH OF THE SKULL	MALES	RANGE OF TOTAL LENGTH OF THE SKULL
Arctocephalus australis	65	13.19-27.13	84	15.30-25.24
Callorhinus ursinus	28	12.85-20.18	23	12.24-25.80
Otaria byronia	133	9.99-25.24	159	12.85-36.71

To analyze ontogenetic allometry, twenty-eight linear dimensions were measured on each complete skull (Figure 1)[15]. For our measure of skull size, we used the condilo-basal length. The other 27 measurements are [y_1, y_2, y_3,…y_{24}] of the allometric vector.

The values of the metrical characters in the individuals were log-transformed. Only specimens with no missing data were used for all analyses. The structure of the covariance matrix of the morphometric variables was studied by the multivariate analysis of Principal Components. The covariance matrices of base-10 logarithmically transformed data were used rather than the correlation matrices because it has been shown that the first principal component of the covariance matrix of logarithmically transformed data best generalizes the allometry equation (COCHARD, 1985). Logarithmically transformed data also tend to make the covariance matrix independent from both the order of magnitude and the scale of the variables, thereby making the final interpretation less complicated (MORRISON, 1976). Log-transformed data may circumvent the problem that PCA describes patterns of covariation among variables based on their magnitude[16] (promotes linearity, SOKAL & ROHLF, 1985) because logarithmic transformation promotes independence of the variance and the mean and in addition. Varimax rotation was included in the PCA to minimize the number of variables that have high loadings on each factor, thus simplifying interpretation of the factors.

Because we used multiple groups we tested if the direction of the maximum variance in the differents groups is the same (NEFF & MARCUS, 1980). This assumption is checked by the vetorial correlation coefficient (calculated separately for each group).

[14] Being ontogenetic rather that static in nature.
[15] The measurements LCS (maximum width of the dentary and LPC (width of the articular face of the condilar process of the dentary) are not exhibited.
[16] The raw variances of variables directly determine the resulting components (PIMENTEL, 1979).



Acronyms: AFM, maximum of height of the forame magnum; AJU, maximum height of the jugal; AOR, maximum width orbit; CBH, basilar hensel length; CCB, basal-condile length; CJU, length of the jugal; CPM, distance between the palate and the forame magnum; CPP, palate length; CRO, rostrum length; CSP, pos-canine series length; DBC, distance between the tympanic bule and the sagital crist; DOM, distance between the optical forame and the forame magnum; DCO, maximum distance between the condiles; DPS, maximum distances between the super-orbital process; LBO, basioccipital width; LCC, maximum width of the braincase; LCO, minimum width at the inter-orbital constriction; LIM, maximum width between the mastoid process; LMP, maximum width of the palate; LON, maximum width of the nasal orifice; LRO, maximum rostrum width; LZI, maximum width of the zygomatic arch; APC, maximum height of the dentary; CDE, maximum length of the dentary; CSD, maximum length of the alveolar process of the dentary; CSM, maximum length of the mandibular synphyse.

Figure 1. Linear measurements taken in the skulls of otarids shown in an adult male specimen of *Arctocephalus australis* in the lateral, occipital, dorsal and ventral view of the skull. The dentary is showed in the medial view only.

To analyze and compare allometric patterns, we used the angles between vectors. A significant correlation between measurements and size could be due to isometry when all coefficients of the vector which describes the correlation of each measurement with centroid size would be equal to one. Thus, the difference between the observed size vector and expected size vector under isometry was quantified as the angle between the vectors. Then, to test if this angle is higher then zero, a bootstrap technique was used (following EFRON & TIBSHIRANI, 1993). For each bootstrap interaction, individual are drawn with

replacement from the original sample and a bootstrap sample was constructed, maintaining the same number of individuals. The size vector of the bootstrap sample is computed and the angle between the bootstrap samples size vector and original sample size vector is calculated. These angles are measured with the aim to determine if the width of confidence interval is less than the angle between the observed size vector and the expected size vector under isometry. If this hypothesis is proved, the observed size vector is judged to be allometric. In this context[17], the coefficients of the morphometrical variables in the PC1 are proportional to the allometirc coefficients of the variables in relation to the multivariate size (STRAUSS, 1985).

This multivariate analysis wasw done on a pooled male and female sample and with samples separated by sex in order to test the hypothesis that all 25 cranial dimensions in the allometry vector grow at the same rate as the internally defined size variable i. e., the null hypothesis of isometric multivariate cranial growth (JUNGERS & HARTMAN, 1988).

Addicionally, we combined the ontogenetic series of all species because the analysis of this data set by PCA can determine if the species diverge over time, retain at a constant distance away or yet converge towards a similar endpoint (ZELDITCH et al., *in press*)

The method to compare directions of vectors between groups was used in the comparison between the vectors of ontogenetic allometric coefficients too[18]. Usually, the vectors are highly correlated just by virtue of a shared increase in overall size (geometric scale), and it is also common that very small angles are significantly different from zero using traditional measurements, because using this kind of variable, the angles are on a very different measurement scale. So, we test how high a vector correlation we could get by randomly permuting the vectors of coefficients. That analysis(testing against a null hypothesis of a correlation of zero, combined with the analysis that compare the directions of vectors against a null hypothesis of an angle of zero (correlation of 1.0)) informs if the angle is significant and if it is, how far from 0 it is. This later procedure was run in Shuffle Allometry (SHEETS, 2000; IMP SERIES) a freeware software disponible at http://www.canisius.edu/~sheets/morphsoft.html. The comparisons between the directions of the ontogenetic allometric vectors were performed between the ontogenetical stages of the same species (to check if only one vector can describe all ontogeny); sexes of the same species and between the females or males of different species[19].

RESULTS

It was shown that the groups share the same axis of major variation because the vectorial correlaction coefficients between the PC1 of each group compared are high (>0.9). Otherwise, allometry was found in both sexes for all species because the growth vectors are different from the vector attempted in a isometric growth ($p<0.05$).

In all species, the first principal component ordinates the specimens according to overall size, which is evidenced by the juveniles that presents the smallest scores and the adults the largest scores. Another evidence is due to the fact that the variable loadings of component I are almost always positive (Tables 2-4), although a wide range of values does exist, indicating that the dimensions does not contribute equally to the first component. Therefore, the first principal component can therefore be interpreted as “a vector of relative

[17] When the first principal component can be understood how an estimative of the general multivariate size
[18] The components of the vectors of ontogenetic allometric coefficients (regression coefficients) for the variables.
[19] The species were compared in pair-wise comparisons

growth" since it shows the direction of size increase along with shape changes that occur in each dimension. Ontogenetic allometry accounts for about 60% of the ontogenetic shape variation in the analysed groups, and static allometry accounts for only 40% of the adult shape variation.

More shape variation is reflected in component II as indicated by bipolar component loadings, i. e., eigenvectors with positive and negative coefficients that could reflects shape changes relative to size increases or growth[20]. Component II scores have a rather tight range between the sexes, and therefore do not separate males from females as nicely as was done anteriorly. This is primarily because females have slightly larger component II scores in the adults than their male counterpart.

When comparing PCAs of males and females separately (Table 2), one can say that the factor loadings of the first principal component, the allometry vector, are quite similar between the sexes except for *O. byronia*.

Arctocephalus australis – The PCA of the females showed Component I to a size component with all positive coefficients and accounted for 77.6% of the total variation. Component II was a shape component and accounted for another 5.57% of the total variation. For the males, the Component I in the PCA was a size component and accounted for 74.8% of the total variation. Component II, a shape component, accounted for a further 5.9% of the total (Table 2).

The juveniles basically varies in the PC1 (25.27%) and the sexes are overlap in the size/shape space. However, the females have their scores more widely distributed in that component (the males are concentrated in the zone of higher score). This scenario change when we compare only adults, where the sexes are perfectly separated in the PC1 (59.39%) and generally far apart in the PC2 (13.83%).

The analysis of the ontogeny of the females and males separately by a Principal Component approach reveals different patterns. The PC1 of the males describes 64.01 of the variation and the PC2 5.9% The females are restricted to a small portion of the PC1 (70.72%) axes and the age classes can be better distinct by the differences in the projections of their scores in the PC2 (8.71%). In that case, the adults have the higher scores in both PC´s and are striking distinguished from the other classes. Besides that panorama we have to consider that in the PC2 is exaggerated in the scatter plot in relation with the portion of the variation that it explains. The juveniles have the smaller scores, overall in the PC2, but they are a few superimposed with the subadults.

[20] The separation of dimensions, sex, or age groups by shape differences relates to dimensions possessing larger positive and negative loadings because positive and negative loadings either increase or decreases with respect to each other as one moves along the second-component axis (SHEA, 1983; 1985) (Tables 2-4).

Table 2. Variables loadings for the two first Principal Component in *Arctocephalus australis* sample for an analysis on the covariance matrix of log-transformed values of the pooled sample of syncranium dimensions (and for males and females separated). *Prp. Totl*. is the percentual of the total variance explained by each component; COEF. Represented the coefficient and K is the multivariate allometric coefficient. The variables more correlated with each component are in bold.

	PC1						PC2		
	SEX POOLED		FEMALES		MALES		SEX POOLED	FEMALES	MALES
	COEF.	K	COEF.	K	COEF.	K	COEF.	COEF.	COEF.
AFM	0.419	0.170	0.342	0.110	0.372	0.148	-0.581	-0.744	-0.672
AJU	**0.937**	1.304	**0.915**	1.244	**0.949**	1.372	-0.021	-0.057	-0.059
AOR	**0.916**	0.510	**0.921**	0.540	**0.912**	0.496	0.042	-0.012	0.062
CBH	**0.985**	0.924	**0.988**	0.883	**0.983**	0.873	0.000	0.098	-0.026
CCB	**0.988**	0.889	**0.985**	0.834	**0.988**	0.859	0.026	0.120	-0.010
CJU	**0.969**	1.111	**0.970**	1.087	**0.968**	1.126	0.092	0.130	0.034
COM	0.765	0.828	0.660	0.387	0.820	1.043	**0.246**	**0.489**	0.143
CPP	**0.943**	1.107	**0.974**	1.224	**0.962**	1.002	-0.101	-0.075	-0.055
CRO	**0.896**	1.122	**0.958**	0.947	0.868	1.213	0.242	0.132	**0.314**
CSP	0.852	0.786	**0.965**	0.625	0.800	0.870	**0.246**	0.146	**0.356**
DBC	**0.979**	0.796	**0.976**	0.741	**0.981**	0.805	0.003	-0.102	0.049
DCM	**0.941**	0.913	0.899	0.889	**0.963**	0.905	-0.007	-0.029	-0.022
DCO	**0.918**	0.555	**0.941**	0.571	0.895	0.532	-0.158	-0.128	-0.245
DPS	**0.914**	1.014	0.894	1.040	**0.948**	0.946	-0.218	-0.350	-0.035
LBO	**0.917**	0.675	**0.936**	0.500	**0.904**	0.616	-0.094	-0.032	-0.023
LCC	0.025	-0.059	0.605	0.399	-0.108	-0.391	-0.474	-0.648	-0.151
LCO	-0.334	0.254	-0.147	-0.355	-0.644	-0.402	-0.700	-0.781	-0.301
LIM	**0.951**	1.227	**0.900**	1.245	**0.981**	1.157	0.067	**0.220**	-0.034
LMP	0.844	0.954	**0.926**	0.968	0.784	0.892	-0.240	-0.183	-0.371
LON	**0.920**	0.050	**0.963**	0.961	0.891	1.007	0.043	0.075	0.032
LRO	**0.967**	1.289	**0.973**	1.156	**0.979**	1.175	-0.120	-0.155	-0.033
LZI	**0.989**	1.007	**0.985**	0.935	**0.992**	1.000	0.045	0.139	-0.021
APC	**0.978**	1.996	**0.978**	1.719	**0.988**	2.118	0.079	0.019	0.052
CDE	**0.986**	1.144	**0.991**	1.087	**0.981**	1.093	0.041	0.100	0.014
CSD	**0.927**	0.642	**0.961**	0.705	**0.894**	0.569	-0.041	0.092	-0.043
CSM	0.770	1.019	**0.951**	1.506	0.605	0.608	-0.300	-0.097	-0.139
LCS	-0.066	0.749	-0.085	-1.692	-0.040	0.849	-0.176	0.127	-0.632
LPC	**0.955**	1.581	**0.904**	1.365	**0.983**	1.666	0.123	0.151	0.048
Prp.Totl	**0.748**		**0.776**		**0.748496**		**0.557**	**0.087**	**0.192**
Eigenvalue	**20.93**		**19.801**		**17.237**		**1.562**	**2.438**	**1.65**

Callorhinus ursinus- The PCA of the females showed Component I to a size component with near all positive (mostly large) coefficients and accounted for 64.67% of the total variation. Component II was a shape component and accounted for another 10.33% of the total variation. In which concerns males, the Component I in the PCA was a size component and accounted for 73.62% of the total variation. Component II, a shape component, accounted for a further 8.94% of the total (Table 3).

Table 3. Variables loadings for the two first Principal Component for an analysis on the covariance matrix of log-transformed values of the pooled sample of syncranium dimensions (and for males and females separated) in *Callorhinus ursinus* sample. *Prp. Totl*. is the percentual of the total variance explained by each component and K is the multivariate allometric coefficient. The variables more correlated with each component are in bold.

	PC1						PC2		
	SEX POOLED		FEMALES		MALES		SEX		
	coefficient	K	coeficcient	K	coefficient	K	POOLED	FEMALES	MALES
AFM	0.570	0.129	0.008	0.076	0,702	0.229	-0,057	**0,794**	-0,268
AJU	0.526	0.274	0.033	0.227	0,711	0.704	-0,512	-0,536	-0,401
AOR	**0.923**	0.381	0.808	0.073	**0,942**	0.610	0,108	0,269	0,078
CBH	**0.965**	0.716	**0.970**	0.149	**0,979**	1.072	0,174	-0,013	0,164
CCB	**0.981**	0.679	**0.985**	0.120	**0,986**	1.008	0,121	0,022	0,105
CJU	**0.980**	0.845	**0.973**	0.224	**0,985**	1.229	0,075	0,032	0,037
CPM	0.752	0.885	**0.927**	0.092	0,717	1.349	**0,409**	0,175	**0,415**
CPP	**0.925**	0.716	0.825	0.217	**0,959**	1.092	-0,036	-0,263	-0,031
CRO	0.881	0.829	0.577	0.237	**0,970**	1.276	0,028	-0,585	0,171
CSP	0.879	0.576	**0.951**	0.011	0,882	0.770	0,187	-0,063	0,246
DBC	**0.956**	0.264	0.881	0.081	0,966	0.334	-0,138	0,126	-0,180
DCM	**0.955**	0.490	0.821	0.060	**0,980**	0.763	0,024	0,395	-0,019
DCO	**0.944**	0.470	**0.931**	0.039	**0,937**	0.649	0,101	-0,038	0,137
DPS	0.828	0.206	0.772	1.136	0,805	0.743	-0,378	-0,159	-0,461
LBO	0.837	0.513	0.664	0.001	0,849	0.615	0,276	**0,332**	**0,422**
LCC	0.569	0.182	0.686	0.016	0,550	0.199	**0,652**	**0,412**	**0,708**
LCO	0.404	0.124	0.059	0.010	0,299	0.021	-0,643	-0,792	-0,687
LIM	**0.964**	0.678	**0.911**	0.026	**0,986**	0.984	0,136	0,031	0,084
LMP	**0.905**	0.702	0.785	0.082	**0,906**	1.011	-0,127	-0,193	-0,085
LON	**0.975**	0.725	0.898	0.198	**0,991**	1.110	-0,002	0,014	-0,035
LRO	**0.960**	0.877	0.860	0.077	**0,983**	1.208	-0,112	-0,168	-0,054
LZI	0.799	0.635	**0.977**	0.101	0,709	0.806	-0,157	0,026	-0,203
APC	**0.943**	0.828	**0.971**	0.154	**0,949**	1.308	-0,169	-0,075	-0,263
CDE	**0.985**	0.791	**0.980**	0.168	**0,991**	1.189	0,035	-0,044	0,011
CSD	0.578	0.311	0.847	0.133	0,537	0.563	-0,274	-0,101	-0,386
CSM	0.724	0.546	0.710	0.148	0,719	0.602	-0,099	-0,134	0,008
LCS	-0.300	0.217	-0.163	0.124	-0,568	0.314	-0,370	-0,495	-0,449

LPC	**0.949**	0.8482	0.946	0.156	**0,942**	1.265	-0,183	-0,055	-0,262
Prp.Totl	0.708		0.647		0,736		0,071	0,103	0,089
Eigenvalue	**19.836**		**18.109**		**20.613**		**1.976**	**2.892**	**2.504**

(Table 3. continuation)

***Otaria byronia*-** Besides the fact that we can identifyer separated groups (without overlapping) only in the adult phase; we can note differences between sexes in terms of spatial pattern in the principal component of all group ages. In the juveniles, the females are more distributed in the second PC (20.65%) and the males in the first one (45.25%) (they are restricted to the higher scores of the PC2). In subadults, both sexes present the same linear distribution pattern (the scores in the two first PCs augment proportionally to each other – PC1=59.223%; PC2=27.591%), but the males have a larger extension (it means, a larger ontogenetic trajectory). Finally, the analysis of the adults shows that the females have lower scores in the PC1 (66.04%) and they present scores largely distributed in the extension of the PC2 (8.49%). However, the males have higher scores in the PC1 and are more concentrated in a median zone of the PC2 axes.

On the other hand, when we analyze the females and males ontogeny, the changes are very different again. In both sexes the scores in the PC1 are related with the age, so the juveniles have the lower and the adults the higher scores in that component. In the females the PC1 explains about 59.32% of the variance and the PC2 explains about 24.84% of the variance. In the males, the PC1 explains about 80.1% of the variance and the PC2 explains about 4.55% of the variance. But in the females, we observe a superposition of the scores of the subadults and adults and a very higher variation in the PC2 during all ontogeny. In the males, the variation increases in early ontogeny and decay later (Fig. 2B) (Table 4).

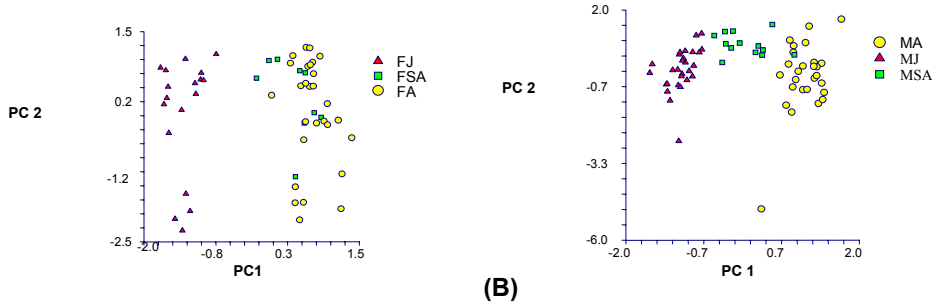


Figure 2. Plottage of the two first Principal Components (PC1 and PC2) of the ontogenetic data of *Otaria byronia*. (A) females (B) males. (A) Females: FJ= juveniles; FSA= subadults; FA= adults (B) Males: MJ= juveniles; MSA=males subadults; MA= adults.

In that species the variable loadings of component II show larger loading differences between the sexes, it seems that principal component II separates the sexes more according to shape than size.

Table 4. Variables loadings for the two first Principal Component for an analysis on the covariance matrix of log-transformed values of the pooled sample of syncranium dimensions of *Otaria byronia* (and for males and females separated). *Prp. Totl*. is the percentual of the total variance explained by each component and K is the multivariate allometric coefficient. The variables more correlated with each component are in bold.

	PC1						PC2		
	SEX POOLED		FEMALES		MALES		SEX POOLED	FEMALES	MALES
	COEF.	K	COEF.	K	COEF.	K	COEF.	COEF.	COEF.
AFM	0.298	0.094	-0.039	-0.040	0.289	0.095	-0.125	-0.113	-0.583
AJU	**0.935**	1.387	0.895	0.690	**0.951**	1.424	-0.070	-0.026	0.145
AOR	**0.957**	0.786	**0.948**	0.314	**0.976**	0.824	-0.131	-0.093	0.057
CBH	0.879	1.171	0.743	0.972	**0.929**	1.156	-0.139	0.111	-0.100
CCB	**0.965**	0.916	**0.968**	0.448	**0.986**	0.947	-0.143	-0.038	0.030
CJU	**0.950**	1.106	**0.970**	0.576	**0.976**	1.144	-0.124	-0.037	0.107
CPM	0.857	0.576	**0.923**	0.253	0.853	0.598	-0.283	-0.088	-0.309
CPP	0.791	1.072	**0.989**	0.686	0.778	1.097	-0.232	0.008	-0.292
CRO	**0.917**	1.099	**0.971**	0.515	**0.912**	1.115	-0.132	-0.051	-0.017
CSP	**0.916**	0.711	**0.962**	0.430	**0.922**	0.713	-0.219	0.023	-0.208
DBC	**0.940**	0.834	**0.955**	0.297	**0.945**	0.858	-0.040	-0.034	0.168
DCM	**0.963**	0.825	**0.958**	0.273	**0.977**	0.858	-0.087	-0.115	0.135
DCO	**0.919**	0.449	0.853	0.183	**0.937**	0.447	-0.106	-0.002	0.008
DPS	**0.940**	1.155	**0.921**	0.461	**0.950**	1.176	-0.038	-0.074	0.228
LBO	0.868	0.588	0.850	0.227	0.891	0.617	-0.282	-0.133	-0.244
LCC	0.676	0.181	0.275	-0.027	0.751	0.194	-0.114	-0.232	0.141
LCO	-0.156	-0.120	-0.724	-0.414	-0.307	-0.129	0.168	-0.158	**0.577**
LIM	0.881	0.899	**0.974**	0.373	0.863	0.967	-0.154	-0.013	-0.157
LMP	**0.944**	1.024	**0.932**	0.392	**0.949**	1.054	-0.151	-0.049	-0.137
LON	**0.930**	0.921	**0.925**	0.365	**0.934**	0.949	-0.055	-0.039	0.106
LRO	**0.967**	1.211	**0.975**	0.487	**0.979**	1.230	-0.115	-0.065	-0.041
LZI	0.898	0.978	0.846	0.552	**0.908**	1.005	-0.117	0.053	-0.033
APC	0.826	1.786	0.174	2.781	**0.975**	1.682	**0.534**	**0.967**	0.164
CDE	0.774	1.213	0.097	1.792	**0.927**	1.161	**0.506**	**0.895**	0.112
CSD	0.808	0.691	0.206	1.084	**0.958**	0.639	**0.494**	**0.923**	0.022
CSM	0.742	1.079	0.012	1.564	**0.942**	1.038	**0.550**	**0.874**	0.063
LCS	0.778	1.295	-0.027	1.695	**0.957**	1.288	**0.537**	**0.883**	0.186
LPC	0.819	1.553	0.158	2.434	**0.978**	1.467	**0.542**	**0.971**	0.121
Prp.Totl	**0.726**		**0.607**		**0.808**		**0.078**	**0.187**	**0.045**
Eigenvalue	**20.335**		**17.006**		**22.616**		**2.180**	**5.249**	**1.272**

Comparative Analysis of the Ontogeny and Allometry between species- When we pooled all specimens together, the linearity of the results obviously decrease strongly (the PC1 accounts for a smaller proportion of the total explained variation, generally). The fur seals are clearly separated from the sea lion, showing a more linear trajectory (and shorter too, in relation to the *O. byronia* pattern). In addition, *O. byronia*

diverge away from the other species over time. In fact, the females of the later present a trajectory similar to that of the fur seals, but their scores in the PC1 (related obviously with size) are higher. *O. byronia* shape changes directions during development, overall in the males. In addition, the males have a longer ontogenetic trajectory, presented scores in the PC1 that were not show by any other subsample. (Fig. 3).

The PC 1 accounted for 46.71% of the total variance and the Component II contributed for 23.9% to the total variance (Table 5). Furthermore, variable loadings of component II show larger loading differences between the sexes and between fur seals and sea lions. It seems that principal component II separates those more according to shape than size (considering all the ages).

Table 5. Variables loadings for the two first Principal Component for an analysis on the covariance matrix of log-transformed values of the pooled sample of syncranium dimensions for the three species examined. *Prp. Totl*. is the percentual of the total variance explained by each component. The variables more correlated with each component are in bold.

VARIABLES	PC1	PC2
AFM	0.375	-0.013
AJU	0.279	-0.891
AOR	-0.471	-0.861
CBH	0.707	-0.483
CCB	**0.936**	**0.175**
CJU	0.564	-0.672
CPM	0.481	-0.187
CPP	**0.889**	-0.032
CRO	**0.847**	-0.337
CSP	0.116	-0.339
DBC	**0.934**	-0.142
DCM	0.461	**0.013**
DCO	**0.877**	-0.055
DPS	**0.782**	-0.047
LBO	-0.230	-0.880
LCC	**0.796**	**0.533**
LCO	-0.569	-0.740
LIM	**0.922**	0.153
LPM	**0.956**	-0.099
LON	0.577	-0.693
LRO	0.053	-0.974
LZI	**0.924**	**0.111**
APC	0.106	-0.741
CDE	**0.807**	**0.171**
CSD	**0.786**	-0.078
CSM	0.738	0.090
LCS	0.195	0.942
LPC	0.275	0.061
Prp. Totl.	**0.4671**	**0.2390**
Eigenvalue	**12.144**	**6.213**

In analyzing only the females, the PC 1 accounted for 46.44% of the total variance and the Component II contributed 14.86 % to the total variance (Table 6).

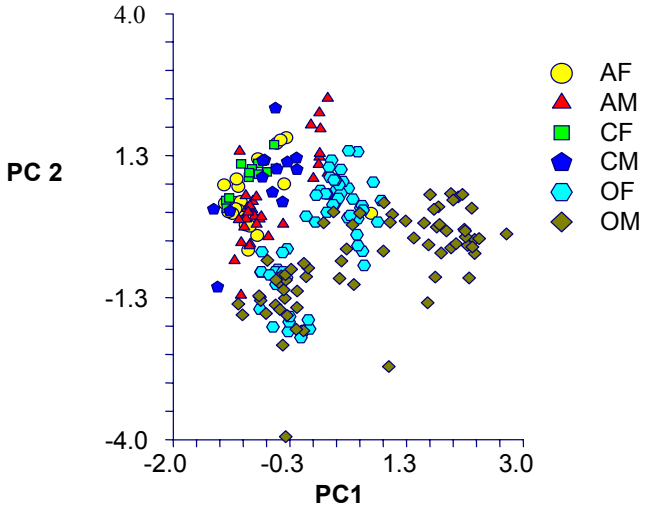


Figure 3. Plot of the two first principal components (PC1 and PC2) of the ontogenetic data of *Arctocephalus australis, Callorhinus ursinus and Otaria byronia*. The scale of y-axis (PC2) is exaggerated to make the separation between groups more visible. AF= A. australis females; AM= *A. australis* males; CF= *C. ursinus* females; CM= *C. ursinus* males; OF= *O. byronia* females; OM= *O. byronia* males.

Table 6. Variables loadings for the two first Principal Component for an analysis on the covariance matrix of log-transformed values of the pooled sample of the syncranium of the females of the three species examined. *Prp. Totl*. is the percentual of the total variance explained by each component. The variables more correlated with each component are in bold.

VARIABLES	PC1	PC2
AFM	0.556	-0.227
AJU	-0.076	**0.937**
AOR	-0.518	0.843
CBH	0.665	0.434
CCB	**0.924**	-0.283
CJU	0.525	0.667
CPM	0.445	0.013
CPP	**0.985**	0.009
CRO	**0.873**	0.350
CSP	0.210	**0.955**
DBC	**0.961**	-0.077
DCM	0.334	-0.070
DCO	**0.931**	-0.152
DPS	0.409	-0.123
LBO	0.333	**0.910**
LCC	0.749	-0.617
LCO	0.646	0.687
LIM	**0.909**	-0.356
LPM	**0.962**	-0.089
LON	0.680	0.637
LRO	-0.249	**0.956**
LZI	**0.903**	-0.309
APC	-0.107	0.155
CDE	0.110	-0.113
CSD	0.128	-0.037
CSM	0.053	-0.057
LCS	0.556	-0.227
LPC	-0.076	**0.937**
Prp. Totl.	**0.474**	**0.1486**
Eigenvalue	**12.333**	**3.863**

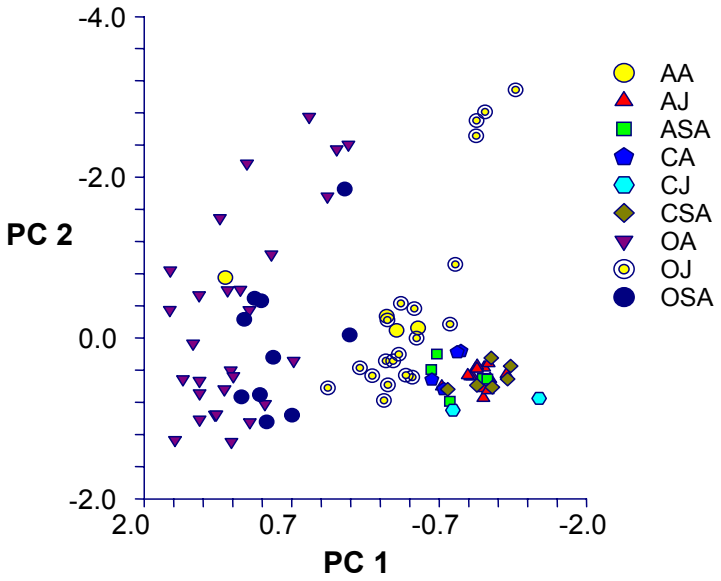


Figure 4. Scatter plot of the two first Principal Components of the ontogenetic data of the females of *Arctocephalus australis, Callorhinus ursinus and Otaria byronia*. The scale of y-axis (PC2) is exaggerated to make the separation between groups more visible. AA= *A. australis* adults; AJ= *A. australis* juveniles; ASA= *A. australis* subadults; CA= *C. ursinus* adults; CJ= *C. ursinus* juveniles; CSA= *C. ursinus* subadults; OA= *O. byronia* adults; OJ= *O. byronia* juveniles; OSA= *O. byronia* subadults.

In analyzing only the males, the PC 1 accounted for 53.49% of the total variance, and the Component II contributed 24.91% to the total variance (Table 7). The PC 1 separes adults and subadults of *O. byronia*, due to size.

Table 7. Variables loadings for the two first Principal Components for an analysis on the covariance matrix of log-transformed values of the pooled sample of the syncranium of the males of the three species examined. *Prp. Totl*. is the percentual of the total variance explained by each component. The variables more correlated with each component are in bold.

VARIABLES	PC1	PC2
AFM	0.281	0.087
AJU	0.354	**0.872**
AOR	-0.524	**0.838**
CBH	0.711	0.507
CCB	**0.962**	-0.122
CJU	0.569	**0.705**
CPM	0.464	0.227
CPP	0.853	0.064
CRO	0.856	0.328
CSP	0.041	0.262
DBC	0.941	0.164
DCM	**0.966**	0.080
DCO	0.865	0.104
DPS	**0.973**	0.114
LBO	-0.237	**0.858**
LCC	0.833	-0.494
LCO	-0.642	**0.697**
LIM	0.796	-0.140
LPM	**0.951**	0.121
LON	0.539	0.735
LRO	0.063	**0.966**
LZI	**0.944**	-0.022
APC	0.133	**0.967**
CDE	**0.969**	-0.061
CSD	0.886	0.185
CSM	**0.925**	-0.029
LCS	0.211	0.917
LPC	0.273	-0.032
Prp. Totl.	**0.534**	**0.249**
Eingenvalue	**13.907**	**6.476**

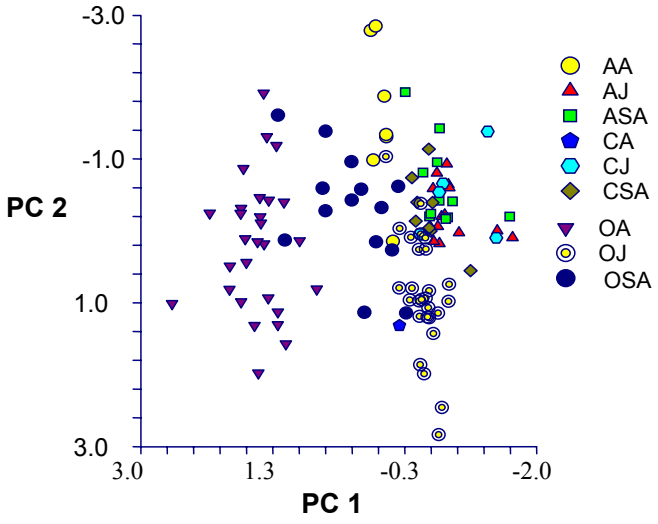


Figure 5. Scatterplot of the two first Principal Components of the ontogenetic data of the males of *Arctocephalus australis, Callorhinus ursinus and Otaria byronia*. The scale of y-axis (PC2) is exaggerated to make the separation between groups more visible. AA= *A. australis* adults; AJ= *A. australis* juveniles; ASA= *A. australis* subadults; CA= *C. ursinus* adults; CJ= *C. ursinus* juveniles; CSA= *C. ursinus* subadults; OA= *O. byronia* adults; OJ= *O. byronia* juveniles; OSA= *O. byronia* subadults.

When we analyze the juveniles of the three species, we found that the PC 1 accounted for 45.44% of the total variance and the Component II contributed 24.31 % to the total variance (Table 8). The PC plot illustrate that essentially *O. byronia* varies in the PC2 and that variation in the PC1 is correelated with size (Fig. 6).

Table 8. Variables loadings for the two first Principal Component for an analysis on the covariance matrix of log-transformed values of the pooled sample of syncranium of juveniles of the three species of otarids examined. *Prp. Totl*. is the percentual of the total variance explained by each component. The variables more correlated with each component are in bold.

VARIABLES	PC1	PC2
AFM	**0.888**	0.163
AJU	-0.758	-0.545
AOR	-0.770	-0.544
CBH	-0.039	-0.307
CCB	**0.902**	**0.230**
CJU	-0.508	-0.648
CPM	0.305	-0.069
CPP	**0.908**	-0.008
CRO	0.423	-0.419
CSP	-0.133	-0.156
DBC	**0.867**	0.019
DCM	**0.930**	0.123
DCO	**0.902**	0.003
DPS	**0.895**	0.064
LBO	-0.693	-0.587
LCC	0.895	**0.321**
LCO	-0.687	-0.555
LIM	0.315	0.142
LPM	**0.934**	0.039
LON	-0.017	-0.968
LRO	-0.708	-0.618
LZI	**0.878**	**0.292**
APC	-0.646	-0.458
CDE	0.472	**0.203**
CSD	0.443	-0.025
CSM	0.351	0.148
LCS	**0.454**	**24.310**
LPC	**12.334**	**3.963**
Prp. Totl.	**0.454**	**0.243**
Eingenvalue	**12.333**	**3.963**

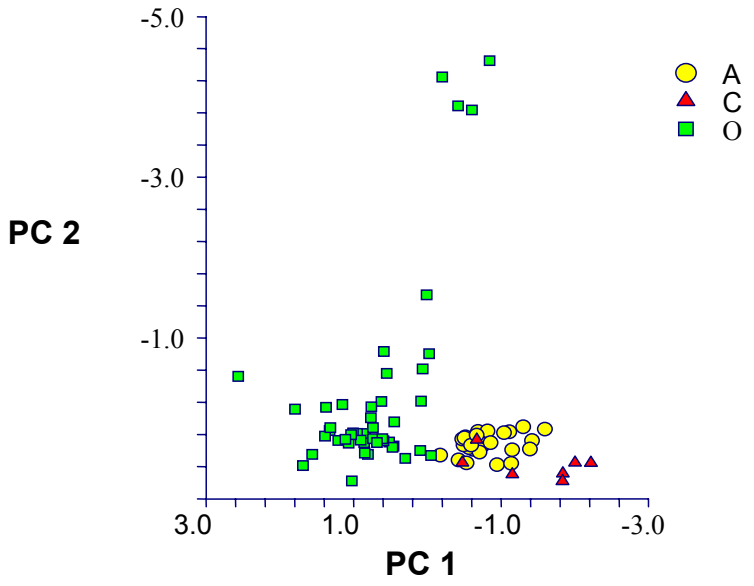


Figure 6. Plottage of the two first Principal Components of the juveniles of *Arctocephalus australis, Callorhinus ursinus and Otaria byronia*. The scale of y-axis (PC2) is exaggerated to make the separation between groups more visible. A= *A. australis* ; C= *C. ursinus*; O= *O. byronia.*

When we analyze the subadults of the three species, we found that the PC 1 accounted for 50.15% of the total variance and the Component II contributed 25.66 % to the total variance (Table 9). The PC plot illustrate a near circular pattern of variation (Fig. 7), but the PC1 is significantly anyway.

Table 9. Variables loadings for the two first Principal Component for an analysis on the covariance matrix of log-transformed values of the pooled sample of syncranium of subadults of the three species of otarids examined. *Prp. Totl*. is the percentual of the total variance explained by each component. The variables more correlated with each component are in bold.

VARIABLES	PC1	PC2
AFM	0.734	-0.239
AJU	-0.014	**0.919**
AOR	-0.556	**0.818**
CBH	0.726	0.264
CCB	**0.922**	-0.338
CJU	0.503	0.395
CPM	0.339	-0.346
CPP	**0.982**	-0.017
CRO	**0.952**	0.195
CSP	0.328	**0.912**
DBC	**0.952**	-0.028
DCM	0.286	-0.052
DCO	**0.936**	-0.130
DPS	**0.980**	0.010
LBO	-0.309	**0.909**
LCC	0.781	-0.576
LCO	-0.617	**0.750**
LIM	0.924	-0.330
LPM	**0.987**	0.009
LON	0.699	0.581
LRO	-0.013	**0.983**
LZI	**0.852**	-0.336
APC	-0.085	0.339
CDE	0.477	-0.199
CSD	0.196	0.018
CSM	0.129	-0.017
LCS	0.195	-0.926
LPC	0.258	0.033
Prp. Totl.	**0.501**	**0.256**
Eigenvalue	**13.039**	**6.670**

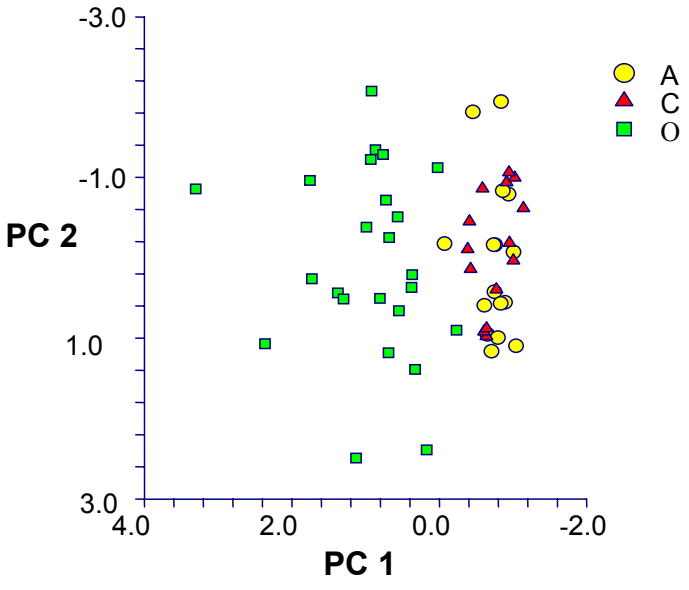


Figure 7. Scatterplot of the two first Principal Components of the subadults of *Arctocephalus australis, Callorhinus ursinus and Otaria byronia*. The scale of y-axis (PC2) is exaggerated to make the separation between groups more visible. A= *A. australis* ; C= *C. ursinus*; O= *O. byronia.*

Finally, when we analyze the adults of the three species, we found that the PC 1 accounted for 47.72% of the total variance for the females and for 64.89% for the males. The Component II contributed for 20.99% of the total variance for the females and for 9.35% for the males (Table 10).

Table 10. Variables loadings for the two first Principal Component for an analysis on the covariance matrix of log-transformed values of the pooled sample of syncranium of adults of *Arctocephalus australis* and *Callorhinus ursinus*. *Prp. Totl*. is the percentual of the total variance explained by each component. The variables more correlated with each component are in bold.

VARIABLES	FEMALES		MALES	
	PC 1	PC 2	PC 1	PC 2
AFM	0.032	-0.035	0.035	0.007
AJU	0.155	-0.118	0.243	0.032
AOR	0.071	-0.085	0.136	-0.013
CBH	0.121	-0.084	0.176	-0.124
CCB	0.125	-0.120	0.168	-0.049
CJU	0.086	-0.072	0.183	-0.057
CPM	-0.061	0.054	0.072	-0.227
CPP	0.299	-0.283	0.241	-0.054
CRO	0.143	-0.148	0.209	-0.135
CSP	0.113	-0.116	0.152	-0.107
DBC	0.134	-0.130	0.174	0.028
DCM	0.119	-0.129	0.172	-0.012
DCO	0.084	-0.067	0.102	-0.023
DPS	0.244	-0.064	0.257	0.069
LBO	0.132	-0.144	0.126	-0.083
LCC	0.034	-0.038	0.042	0.007
LCO	0.007	-0.050	0.012	0.047
LIM	0.116	-0.124	0.174	-0.133
LPM	0.216	-0.231	0.223	-0.004
LON	0.144	-0.153	0.192	-0.033
LRO	0.225	-0.242	0.250	-0.053
LZI	0.128	-0.082	0.173	-0.081
APC	0.415	0.200	0.323	-0.047
CDE	0.212	0.161	0.207	-0.080
CSD	0.199	0.030	0.138	0.011
CSM	0.315	0.095	0.222	0.012
LCS	0.268	0.705	0.211	0.917
LPC	0.335	0.187	0.273	-0.032
Prp. Totl.	**47.727**	**20.994**	**64.8919**	**9.352**
Eigenvalue	**0.177**	**0.078**	**0.247**	**0.035**

Pairwise Comparison between Arctocephalus australis and Callorhinus ursinus - The ontogeny of *C. ursinus* is more linear in comparison with *A. australis* where the specimens are distributed widely in the scatter plot area. The females of *C. ursinus* are restricted to an area of the scatter plot where we observe a large overlap between the groups (males and females of both species) (Fig. 8). The component I in the PCA accounted for 73.35% and the component II accounted for 5.74% of the total variation (Table 11).

Table 11. Variables loadings for the two first Principal Component for an analysis on the covariance matrix of log-transformed values of the pooled sample of syncranium of *Arctocephalus australis* and *Callorhinus ursinus*. *Prp. Totl*. is the percentual of the total variance explained by each component. The variables more correlated with each component are in bold.

VARIABLES	PC 1	PC 2
AFM	0.459	0.465
AJU	0.785	0.040
AOR	0.864	0.099
CBH	**0.975**	-0.020
CCB	**0.980**	-0.027
CJU	**0.906**	0.052
CPM	0.675	0.067
CPP	**0.899**	-0.088
CRO	0.884	-0.221
CSP	0.832	-0.276
DBC	**0.973**	-0.024
DCM	**0.939**	0.031
DCO	**0.900**	0.193
DPS	**0.897**	0.150
LBO	0.521	0.295
LCC	0.103	0.515
LCO	-0.162	**0.747**
LIM	**0.943**	-0.062
LPM	0.817	0.045
LON	**0.931**	0.041
LRO	**0.962**	0.058
LZI	**0.943**	-0.054
APC	**0.960**	-0.145
CDE	**0.930**	0.070
CSD	0.753	-0.161
CSM	0.754	0.124
LCS	0.142	-0.099
LPC	**0.951**	-0.136
Prp. Totl.	**0.674**	**0.051**
Eigenvalue	**18.878**	**1.449**

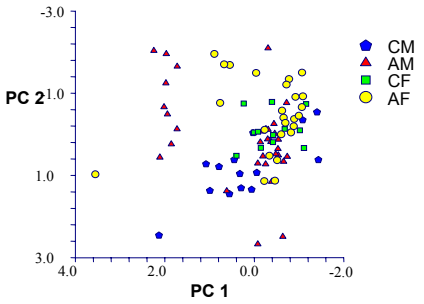


Figure 8. Pairwise comparison of factor I and II from the principal component analysis of *A. australis* and *C. ursinus* (identified by sex). CM= *C. ursinus* males; AM= *Arctocephalus australis* males; CF= *C. ursinus* females; AF= *A. australis* females.

Pairwise comparison between Arctocephalus australis and Otaria byronia - When we perform a comparison pooling *A. australis* and *O. byronia,* Component I accounted for 73.35% of the total amount of variance and the Component II accounted for 5.74% of it (Table 12). The pattern is a few similar with that of the three species pooled together. The two species are distributed in different areas of the shape and size space. The first species occupies a smaller area of the scatter plot (and the males occupy a larger are of the

PC2 axes in relation of the females of the same species). In *O. byronia,* we denote that the females vary more along the PC2 and the males along the PC1 (Fig. 9). The coefficient of the measure CPM in the PC2 is related with the big difference between species in the extension of the bone palate.

Table 12. Variables loadings) for the two first Principal Component for an analysis on the covariance matrix of log-transformed values of the pooled sample of syncranium of *Arctocephalus australis* and *Otaria byronia*. *Prp. Totl*. is the percentual of the total variance explained by each component. The variables more correlated with each component are in bold.

VARIABLES	PC 1	PC 2
AFM	0.487	-0.275
AJU	**0.947**	0.065
AOR	**0.958**	0.114
CBH	0.874	0.219
CCB	**0.972**	0.143
CJU	**0.951**	0.192
CPM	0.641	**0.535**
CPP	0.861	0.115
CRO	**0.926**	0.132
CSP	**0.931**	0.156
DBC	**0.960**	-0.039
DCM	**0.973**	0.006
DCO	**0.938**	-0.091
DPS	**0.955**	-0.103
LBO	0.834	0.050
LCC	0.674	-0.345
LCO	0.080	-0.770
LIM	**0.898**	0.098
LPM	0.954	0.021
LON	**0.949**	0.006
LRO	**0.974**	0.012
LZI	**0.922**	0.114
APC	0.872	-0.184
CDE	0.822	-0.198
CSD	0.871	-0.213
CSM	0.821	-0.328
LCS	0.383	-0.228
LPC	0.866	-0.180
Prp. Totl.	**0.674**	**0.051**
Eigenvalue	**20.539**	**1.449**

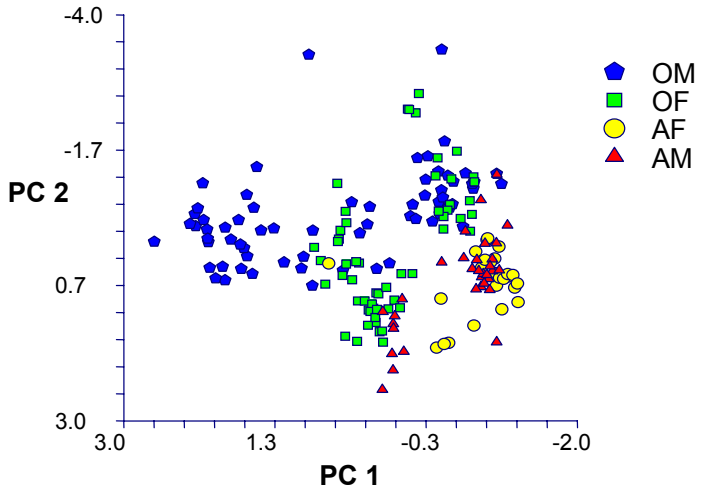


Figure 9. Pairwise comparison of factor I and II from the principal component analysis of *Arctocephalus. australis* and *Otaria byronia* (identified by sex). OM= *O. byronia* males; OF=*O. byronia* females; AF=*A. australis* females; AM=*A. australis* males.

Pairwise comparison between Callorhinus ursinus and Otaria byronia – Again, the males of *O. byronia* present a different orientation in comparison with females (Figs. 5 and 6) and *C. ursinus* and the females of the former presents larger coefficients in the PC1 that the specimens of the later species (Fig. 10). The Component I from the PCA accounted for 71.26% and PC2 accounted for 6.22% of the total variation in shape and size, being the females of *O. byronia* the group that presents the largest variation in that component (the males are very restricted in PC2 varying basically in the PC1) (Table 13) (Fig. 10). Again, the coefficient of the measure CPM in the PC2 is related with the big difference between species in the extension of the bone palate.

Table 13. Variable loadings for the two first Principal Components for an analysis on the covariance matrix of log-transformed values of the pooled sample of syncranium of *Callorhinus ursinus* and *Otaria byronia*. *Prp. Totl*. is the percentual of the total variance explained by each component. The variables more correlated with each component are in bold.

VARIABLES	PC 1	PC 2
AFM	0.432	-0.023
AJU	**0.917**	0.079
AOR	**0.949**	0.160
CBH	0.866	0.179
CCB	**0.971**	0.145
CJU	**0.919**	0.213
CPM	0.500	**0.510**
CPP	0.840	0.132
CRO	**0.931**	0.105
CSP	**0.930**	0.132
DBC	**0.954**	-0.007
DCM	**0.972**	0.056
DCO	**0.930**	0.047
DPS	**0.951**	-0.034
LBO	0.897	0.192
LCC	0.734	-0.005
LCO	0.014	-0.391
LIM	0.880	0.129
LPM	**0.953**	0.058
LON	**0.948**	0.023
LRO	**0.973**	0.061
LZI	**0.903**	0.120
APC	0.850	-0.429
CDE	0.804	-0.403
CSD	0.840	-0.415
CSM	0.796	-0.471
LCS	0.264	-0.381
LPC	0.845	-0.428
Prp. Totl.	**0.712**	**0.062**
Eigenvalue	**29.951**	**1.740**

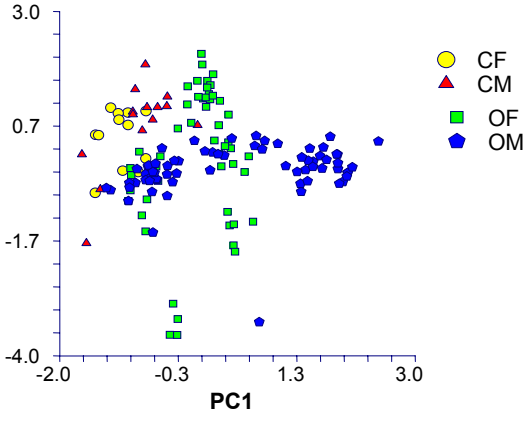


Figure 10. Pairwise comparison of factor I and II from the principal component analysis of *Callorhinus ursinus* and *Otaria byronia* (identified by sex). CF= *C. ursinus* females; CM= *C. ursinus* males; OF= *O. byronia* females; OM= *O. bryonia* males.

Comparisons of the directions of the allometric vector- A vector correlation coefficient of 0.945519 (*Arctocephalus australis*) and 0.903335 (*Callorhinus ursinus*) indicates similarity between the sexes given the rather large difference on explained variance by respective first components. In O. byronia, the angle within females is 25.1 degrees (the values for the correlation at 97.5 th percentile value is 0.666; the mean is 0..48 and the maximum value over 400 shufflings was 0.801). The angle within males is 9.9 degrees (the values at 97.5 th percentile value is 0.781; the mean is 0.652 and the maximum value over 400 shufflings was 0.841). However, the angle between the samples (females versus males) is 12 degrees (which corresponds to a correlation coefficient of 0.875). Nevertheless, when we permute randomly the vectors of coefficients of each sex testing against a null hypothesis of a correlation of zero we find that the angle is not so far from zero. Males when compared to males of another species are no more different than expected by chance (and the same is valid for the females). Furthermore, we did not find differences between the allometric vectors of males and females of *A. australis* or either for *C. ursinus*. In the same way, the ontogenetic trajectory of all groups is apparently linear: a unique allometric vector describe adequately the ontogeny (they are not changes in directions of changes in development).

DISCUSSION

Comparative studies of ontogenetic allometries serve two primary purposes. First, they test general theories about the relationship between form, function and development, due to the great developmental significance of the ontogenetic allometry. Second, comparative studies test theories about the evolution of development and the impact of evolving developmental systems on morphological diversity. Explanations of morphometric evolution that invoke latent variables assume that correlated variation in anatomical dimensions is caused by unobserved (and therefore unmeasured) factors (CRESPI & BOOKSTEIN, 1989). General size, an important element in most causal models for morphometric data analysis, represents the totality of genetic and environmental factors with general effects on growth; if growth is disproportionate; general-size coefficients must reflect allometry for the residual variation to be biologically interpretable (WRIGHT, 1932).

It is logical that the PC1 is strongly correlated with size and that it was detected that size describes most of the shape changes during growth considering that the specimens studied conform to an ontogenetic series with a large size range, but evidently, there is some shape also incorporated into the first component (MOSIMANN, 1970; MASTERSON & LEUTENEGGER, 1989). In the males (pooled samples of the 3 species), basically only *O. byronia* vary in that component, in a perfect congruence between the loadings and the ontogenetical stages.

Additionally, there are good theoretical reasons to expect large and small animals to differ in shape. Simple mechanical principals predict changes in proportions as size changes. These scaling rules predict changes in proportions during growth and differences in proportions among individuals at the same stage of growth (HUXLEY, 1932). Evolutionary changes also are expected to follow these scaling rules (SWARTZ, 1997).

According to D´Arcy Thompson “We rise from the conception of form to an understanding of the forces which gave rise to it” Studies of functional morphology contribute in several ways to the understanding of evolutionary patterns and processes. The former include the unraveling of dependencies of characters and the construction of biomechanically feasible transformation schemes. Among the latter are the

identification of structural novelties that facilitate a cascade of diverse structural changes, and the identification of mechanisms that enable the incorporation of evolutionary novelties in the integrated organism. The study of mechanisms that maintain the match between form and function during evolutionary (and developmental) changes is a new and important area for evolutionary biologists (GALIS, 1996).

When we analyzed each species, we verify that ontogenetic allometry is still the dominant axis of ontogenetic shape variation and that static allometry does not represent a meaningful proportion of adult shape variation.

O. byronia expressed marked sexual dimorphism (males larger than females) in all variables relatied to robusteness and most variables relating to rostrum were also larger in the males. Sexual dimorphism is pronounced in variables relating predominantly to breadth or robusteness of the skull in the fur seals too, but in a lower intensity.

From as early as the time of Darwin (1859), evolutionary biologists have been intrigued by secondary sexual dimorphism. Indeed, the mechanisms giving rise to secondary sexual dimorphism, as well as its consequences, continue to be of interest to systematists, geneticists and ecologists alike. The relation between secondary sexual dimorphism and polygamous mating systems, differential maturation rates and dissimilar resource utilization is critical to a number of evolutionary theories. Nonetheless, confusion exists as to what characteristics are ultimate factors selecting for dimorphism and which are secondary effects of the dimorphic condition (WILLIG & HOLLANDER, 1995).

A very important point to note here is that, altoug the allometric vectors of females and males presented a correlation of more that 0.97, they differ significantly (i.e., the correlation is lower than 1) but they are yet more similar than expected by chance (i. e., the correlations are higher than zero). It seems counter intuitive for such a high correlation to be no greater than expected by chance, but this is often the case in studies based on traditional morphometric data (and this is why it is important to take care when we infer allometry based only in the correlation of a set of linear measurements and the linear measurement that represents general size).

In effect, what we found in the comparison between the allometry of females and males of *O. byronia* is that the angle between the two sexes growth vectors is larger than can be achieved by random division of a single sex, so the two vectors are distinct. The different vectors reflect a statistically significant ($p<0.05$) difference in the patterns, given the sample sizes. Additionally, the angle between the two species growth vector is smaller than expected by random permutations of the allometric coefficients, so that the two vectors have more in common than one would expect by completely randomly permuting the coefficients. In summary, there is a statistically meaningful difference in the trajectories, but a smaller difference than would be expected if the growth trajectories of the two species were completely unrelated to one another (totally randomly permuted).

It should be considered that the point at which two trajectories are dissimilar enough to no longer be considered as conserved is a difficult and probably data-specific problem. As the number of variables in an analysis increases, as smaller average change in the allometry of each is required to yield significant differences between whole vectors.

Measurements with negative allometry are related with the neural system (e. g. AFM, LCC) or with the development of the muscles during ontogeny (LCO). In *A. australis* AJU, CJU, COM (only in the males), CPP, CRO (only in the males), LIM, LRO, LZI and the most of the measurement taked in the dentarium (except CSD and LCS) are positively alometric. But in O. byronia, in one side we note that the positive

allometry is more general, but in the other side that allometry is more strong in males, specially in the measurements AJU, CBH, CJU, CPP, CRO, DPS, LMP, LRO and int the dentarium (except in CSD, obviously). Females presents allometric coefficients positives basically in the dentarium. In that scenere, it is possible to perceive that the development of process is very allometric. In *C. ursinus*, positive allometry in present in males.

Vectors of postweaning craniometric ontogeny are very nearly parallel inlog-measurement space, and morphological divergence accompanying speciation must therefore be accomplished by other developmental mechanisms than post-weaning relative growth rates. Explanations for this result could reasonably invoke simple developmental models that predict negative covariances between anatomically adjacent measurement variables (RISKA, 1986). Such covariances might be revealed by analyses of secondary factor structure within samples (VOSS & MARCUS, 1992). Adaptative interpretations may be appropriate for many vectors of size-adjusted differences between populations and species, but testing such interpretations is difficult and alternative, nonadpative explanations of interspecific character covariance should also be considered. An important but unexamined issue in many evolutionary and systematic studies, especially those that involve morphological comparisons at lower taxonomic levels, are whether observed sample differences reflect evolved genetic values or represent the environmentally induced responses of plastic phenotypes.

CAPÍTULO II

DEVELOPMENT AND GROWTH IN OTARIDS: A MORPHOMETRIC COMPARATIVE STUDY

DEVELOPMENTAL AND GROWTH IN OTARIDS: A MORPHOMETRIC COMPARED STUDY

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ABSTRACT

We examine three Otariidae species: *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia* with the objectives of (1) accessing the developmental and growth rate of males and females and compare it; (2) to describe the skull development for each linear measure for ead species and sex; (3) to stablish the parameters and respective equations (4) to determine which are the variables that are better correlatd with the ages; (5) to determine the physical maturity of the skull. We employed traditional and geometrical morphometric techniques and we verified strong differences between the two approaches due to the particularities of each one. However, in both treatments, a relationship between size dimorphism and shape dimorphism can be infered in the skull of each one of the studied groups. Otherwise, females are generally more accelerated and the males growth for a longer time, but the relationships between the ontogenies and phylogenies were not clarified by our results in any approach.

INTRODUCTION

Contemporary and traditional classifications of higher vertebrates are based in large part on assessments of similarity in adult structure of living and fossil forms. Interpretation of differences in size and shape of homologous structures in different taxa like a result from differences in rates and timing of growth and development is almost axiomatic (ALBERCH, 1980).

Obviously, the different growth patterns observed in the skull of animals have a significant influence in morphogenesis and the production of the final form (RICHTSMEIER et al., 1993). These are usually determined not only by an individual´s genome, but by an array of environmental factors that functionally influence the growth of certain regions (HERRING, 1993). Developmental processes produce morphological variation and constraints and consequently affect evolutionary processes in two principal ways. Because they determine the growth curves, they influence the extent to which values of the same trait at different ages can vary independently (CHEVERUD et al., 1983). Growth processes not only produce variation in morphometric traits, but they can also eliminate it by compensatory growth, such that all individuals converge toward a “target” size as adults (KLINGENBERG, 1996). Sometimes, it is possible that compensatory modifications in rate and duration occur such that rates of growth are decreased relative to time, whereas the duration of that interval is extended in time, and the rate of development (relative to growth) is unmodified. The result would be an unmodified size at maturity and an unmodified rate of development relative to size, but the duration of postnatal growth would be different. To detect that kind of compensatory changes chronological age information is required (ZELDITCH et al., 2001).

Another very interesting approach is that the degree of skull shape maturity appears to be a remarkably good predictor of “ecological maturity.” We may be able to use it to infer life-history strategies (ZELDITCH, 2003b).

Additionally, growth is very linked with sexual dimorphism, overall in what concerns size and PC1 sexual dimorphism is known in a large number of pinnipeds species. Despite that fact, sometimes the sex determination of skeletons and skull is not easy (SCHILLER, 2000).

Sexual size dimorphism is produced proximately by differences in patterns of growth between the sexes; thus, selection acting on the growth of males and females will result in changes in sexual size

dimorphism of adults. Otherwise, recent studies of sexual dimorphism in large, terrestrial, herbivorous mammals and primates have suggested that an investigation of its ontogenetic bases may provide new insights (and information not obtainable from studies concerned only with adults). An ontogenetic approach to sexual dimorphism is essential because 1) it is the entire pattern of sex-differentiated growth and not merely the adult end points, which is adaptative and the target of selection, and 2) a given adult may be produced by very different developmental processes, indicating selection for quite different factors (LEUTENEGGER & MASTERSON, 1989).

In addition, growth studies offer one method of investigating the developmental pathway of an organism and the ways in which that pathway might be altered (FIORELLO & GERMAN, 1997). For example, some studies aim to reveal the growth mechanisms that lead descendants to become different from their ancestors. We notice that the study of somatic growth is of great value for the knowledge of the biology of the species, since the phenomenon of growth is the end product of biochemical, physiological and organic processes (BARRETO et al. 2001).

Furthermore, besides the fact that growth curve parameters can be an efficient tool for the of analysis sex-linked and intra and interspecific differences in body size (e. g., McLAREN, 1993), it provides an index by which temporal changes within a population can be measured (GARLICH-MILLER & STEWART, 1998). Additionally, the quantitative description of growth curves for morphometric traits gives a basis for assessing the ontogenetic patterns underlying differences in morphological structure (CREIGHTON & STRAUSS, 1986). Another advantage of growth curves is the fact that the utilization of mathematical models in growth studies allows its parameterization, so growth patterns from different populations can be compared statistically. Growht has been modeled in several ways, , where we note the asymptotic models of von Bertalanffy, Gompertz, logistic and Richards. But for be a useful tool for the comparison of data on growth and development among taxa the choicen model should be precise in terms of the description of the growth, and equally flexible (CREIGHTON & STRAUSS, 1986).

Finally, it is important to mention that variation in neonatal maturity among mammals is usually explained by variation in gestation length, but species may also be distinct in terms of developmental rate and the later have long been of interest in studies relating morphogenesis to life history, overall in the literature about heterochrony. GOULD (1977) postulated that selection on developmental rate or timing might lead to predictable changes in adult morphology via indirect effects on morphogenesis, and the classical formalism of ALBERCH et al. (1979) is surely useful as a heuristic device. However, it is a problematic analytic tool because it makes two questionable assumptions about morphogenesis: (1) the ontogeny of shape can be represented by a simple linear vector; (2) species share the same trajectory of form (GOULD, 1977; RICE, 1996). The first assumption is rarely rigorously tested (ZELDITCH et al, 1993b) and the assumption of the conservatism of morphogenesis is open to question (SHEA, 1983; REIS et al., 1988; O'HIGGINS et al., 2001; SINGLETON, 2002).

Here, we examine three species: *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*. *Callorhinus ursinus* is supposedly the extant otarid closer to the ancestral of the Otariidae family and *O. byronia* seems to be the more derived (BERTA & DEMERÉ, 1986). The southern sea lion (*Otaria byronia*) females attain sexual maturity between 3-4 years old and the males between 5-6 years old (VAZ-FERREIRA, 1981). But on the other hand, DANS (1993) presents more histological evidences for her conclusions about that issue and she found that the females mature around 5 years old (about 140 cm of total length) and the males at about 7 years old (around 200 cm of total length) The south American fur seals

(*Arctocephalus australis*) females attain sexual maturity approximately with 3 years and the males about 7 years (VAZ-FERREIRA & PONCE DE LÉON, 1987). However, CORCUERA (1989) demonstrated that the females of this species matures near 2 or 3 years old (about 130 cm of total body length; Daniza SCHILLER, personal communication) and the males when they attain around 150-160 cm of total length (between 9 and 13 years old; SCHILLER, unpublished data). Finally, the northern fur seal (*Callorhinus ursinus*) females attain sexual maturity between 3 and 7 years (140 cm of total length) and the males about 5 years old (210 cm of total length) (LANDER, 1981) .

In that context, our principals goals are (1) to access the developmental and growth rate of males and females of 3 species of otarids and compare the revealed results; (2) to describe the skull development for each linear measure for ead species and sex; (3) to stablish the parameters and respective equations (4) to determine which are the variables that are better correlatd with the ages; (5) to determine the physical maturity of the skull.

MATERIAL AND METHODS

Data- Our sample comprises cross-sectional ontogenetic series of skull of the three otarid species mentioned above (Tables 1 and 2).

Table 1. Characterization of the studied sample (traditional methods). The lengths are in centimeters.

	FEMALES	RANGE OF TOTAL LENGTH OF THE SKULL	MALES	RANGE OF TOTAL LENGTH OF THE SKULL
Arctocephalus australis	65	13.19-27.13	84	15.30-25.24
Callorhinus ursinus	28	12.85-20.18	23	12.24-25.80
Otaria byronia	133	9.99-25.24	159	12.85-36.71

Table 2. Characterization of the studied sample (geometrical methods). Centroid size are in in centimeters.

	FEMALES	SIZE RANGE OBSERVED IN UNITS OF CENTROID SIZE	MALES	SIZE RANGE OBSERVED IN UNITS OF CENTROID SIZE
Arctocephalus australis	37	18.9332-37.3608	39	23.5996-43.948
Callorhinus ursinus	25	21.0265-40.6728	26	21.4542-46.9817
Otaria byronia	37	14.8127-47.0011	47	22.0856-57.6586

Analysis employing traditional (linear) measurements- A total of 22 linear measurements were employed. Data for each sex were examined independently to test for sexual dimorphism (MANSFIELD, 1958) (Fig. 1).

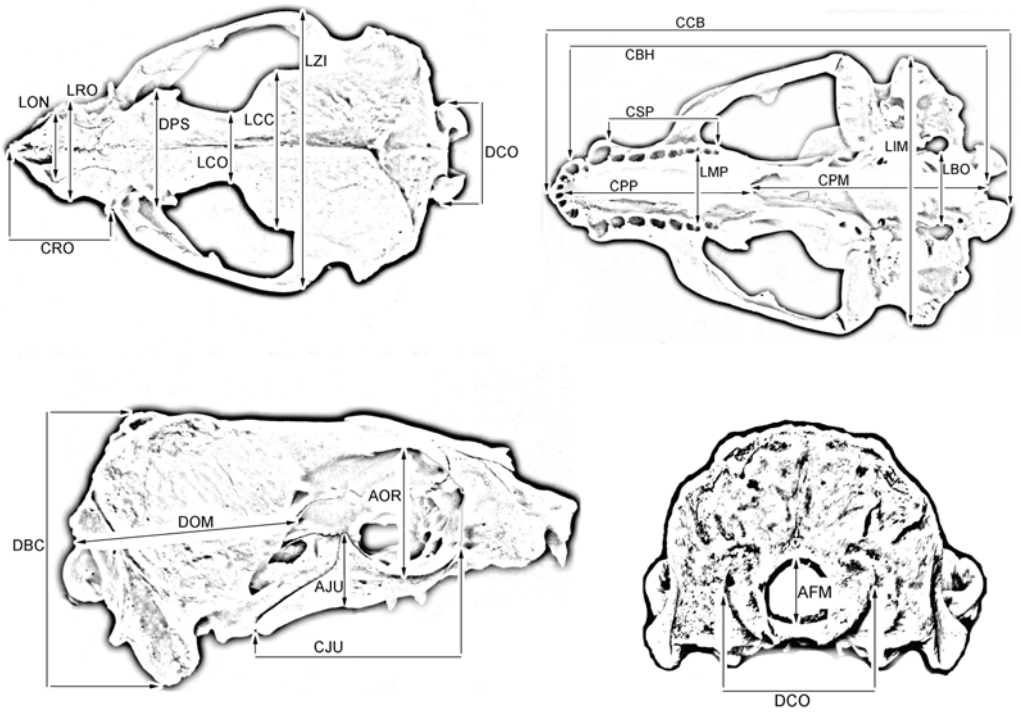

Figure 1. Linear measurements taken in the skulls of otarids exhibit in an adult male specimen of *Arctocephalus australis* in the dorsal, ventral, lateral and occipital view of the skull. For the acronyms see the Appendix 1.

Ages were estimated from upper canine teeth. The teeth were cut in the half tooth, etched in formic acid 5% and rubbed with graphite powder (PIERCE & KAJIMURA 1980; ROSAS et al. 1990; SCHIAVINI et al. 1992; SCHILLER 2000). The Growth Layer Groups (GLGs) in the dentine and cementum of the teeth were counted. We interpreted each GLG as equivalent to one year's growth (PERRIN & MYRICK 1980; SCHIAVINI et al. 1992).

The Gompertz (McLAREN, 1993) equation describes the skull growth for each linear variable in agreement with the sex and to establish the parameters and equations to determine which variable were better related with age. It is customary to use the Gompertz growth curvepartly because those models fit a large number of species (if not all of them equally well) that they offer a general framework for comparison (Miriam Zelditch, personal communication). Besides that, some variables is not fitted by the model and the respective parameters were not calculate due to the redundancy presented.

This equation is expressed by:

$$S_t = A_\infty \times e^{-e^{-k(t-t_0)}}$$

Were: S_t, is the value of each measurement in each age t; t is the amount of time measured in years (GLGs); A_∞ is the asymptotic value of variables; k is the growth coefficient, t_0 is the hypothetical age in which the species would have had length equal to zero; (e.g., the average length the species would reach if it grow indefinitely), and e is the base of the natural logarithm.

The adjustment of the growth models to the data was done minimizing the sum of squared residuals using the interaction quasi-Newton method (module non-linear) of the Program Statistics 5.0. for Windows. The growth curves were calculated for males and females, respectively.

To establish the age of physical maturity of the skull in each curve, we used the age when the asymptotic length of the measurements that are highly correlated with age[21] had attained 95% of the total (A_∞ * 0.95) as an indicator of the length of the growth period and as an index that can be used to compare growth patterns between sexes (GARLICH-MILLER, 1998). In agreement with the former authors, the age of physical maturity (t) of skull was determined by a visual analysis in each variable in relation to the age of the stabilization of the growth curve (asymptote) in the variable that presented the higher determination coerfficient ($r^2 \geq 0.90$) in the growth curves constructed.

In this work when (t) was different for each variable, we used the mean the all ages of attainment of physical maturity for the variables selected with ages of attainment of physical maturity.

To test for sexual dimorphism, male and female growth curve asymptotes were compared using a t-test for unequal sample sizes and unequal variances (GLANTZ, 1992). Sex-related differences in growth rates were described by polling the differences in predicted length between male and female models as a function of age[22].

Geometric Morphometrics Analysis- To examine the ontogeny of shape we use additionallly a landmark based geometric morphometrics because GOULD'S (1977) clock model and ALBERCH et al.'s schemes (1979) are both, based on a geometric conception of shape.

Landmarks are sampled on the ventral view of the skull, which provides information about both trophic and cranial morphology. Skulls photographed with the bone palate oriented parallel to the photographic plane, and digitized on both right and left sides. Bilaterally homologous landmarks were averaged to avoid inflating degrees of freedom. Landmarks sampled on skulls of the specimens are shown in the figure 2. Landmark configurations are superimposed using the generalized least squares superimposition, which preserves all information about shape differences among specimens, removing only information unrelated to shape (i.e. scale, position and orientation; ROHLF & SLICE, 1990). As this procedure produces more variables than there are dimensions of shape, statistical analyses are performed on variables obtained by a rigid rotation of those data, i.e. partial warp scores, including the scores of the uniform component (BOOKSTEIN, 1989; 1991).

[21] $r \geq 0.85$

[22] ΔPredict length=Predict length of the males – Predict length of the females

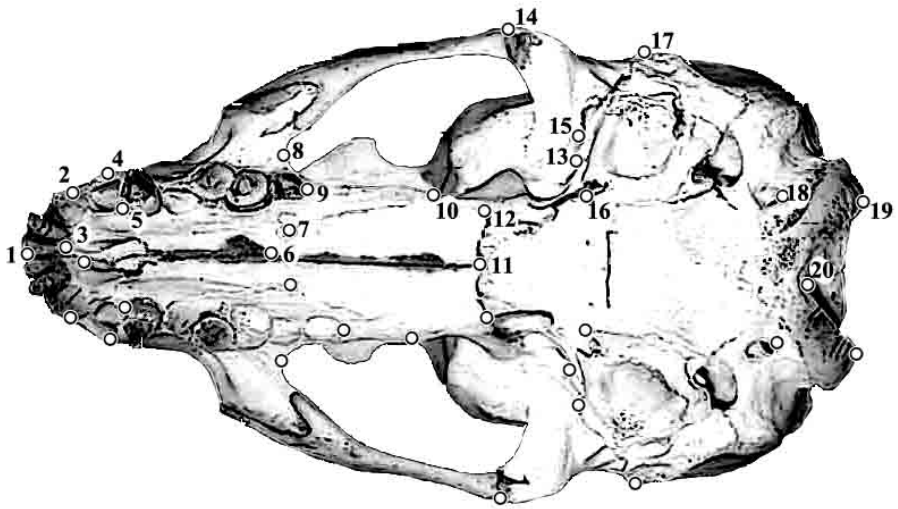

Figure 2. Landmark positions in the ventral view of the skull of a juvenile *Otaria byronia*. The anatomical description of the landmarks is in the appendix 2.

To estimate rates of maturity, it is important that samples be large enough to allow for estimating the mean shape for each age reliably. To estimate rates of development, we measure the rate at which shape gradually differentiates away from that of the stage at which skulls are first sufficiently ossified to measure. The degree of differentiation is measured by the morphometric distance between each individual and the average of the youngest age class (juveniles with sutural age 9 or 10), using the Procrustes distance, (BOOKSTEIN, 1996). Growth rates are estimated by the rate of increase in centroid size. We use that metric to compare the three otarid species focused.

To estimate the rate and timing parameters, eight standard growth models are fitted to the Procrustes distances and centroid sizes: (a) the flexible Chapman–Richards model, (GAILLARD et al., 1997); (b) the monomolecular model, GAILLARD et al. (op cit.); (c) the von Bertalanffy model (ZULLINGER et al. 1984); (d) the Gompertz model (ZULLINGER et al. op cit.); (e), the German Gompertz model (FIORELLO & GERMAN 1997); (f) the logistic model GAILLARD et al. (op cit.); (g) a quadratic function; and (h) a linear function (for each equation see ZELDITCH et. al. 2003 - Appendix 1). Models are fitted to data using the Nelder–Mead simplex with a least-squares error criterion (PRESS et al., 1992). This procedure, similar to a maximum likelihood model, assumes that residuals are normally distributed and independent. To check if the data meet that assumption, we examine the residuals for evidence of autocorrelation. Models exhibiting statistically significant autocorrelations of residuals are rejected for further consideration. The others are evaluating in terms of percentage of variance explained[23] and then we evaluate in terms of their relative goodness of fit (employing the Akaike information criterion (AIC), an estimate of the Kullback–Liebler information distance between the data and the model (AKAIKE, 1974). The AIC score balance the likelihood of the parameters given the data and the number of parameters in the model (complexity). AIC weight (calculated from the AIC scores), represents an estimation of the relative probability that a given model is correct, providing a criterion for model choice.

Using the best-fitting model, we calculated the parameters for development and growth, placing confidence intervals on the parameters by bootstrap. The relative degree of maturity (in both size and shape) is then estimated from the parameters of the best fitting model (by predicting the values for each age and

[23] To test by bootstrap if the observed fit of the models to the data really exceeds that expected by chance.

estimating the proportion of adult maturity or adult size attained at a due age). To determine relative grade of shape and size maturity for each given age and to determine the time of development and growth in each species/sex group we measure the length of the vector over a range of ages (here, one year) and compare that for each species/sex group. This can be also be done by estimating the Partial Procrustes Distances between of two comparable shapes that are separated by one year of age and place confidence intervals on that distance. So we can check if the distances differ significantly in each year of the ontogeny, and by how far they are different.

The calculation of the variance explained by the model, the significance of the autocorrelations, the parameter estimation and calculation of confidence intervals, the model evaluation itself and the estimation of maturity in size/shape are estimated/calculated by GrowChoice – IMP series (SHEETS, 2000).

The differences between rates of change in males and females of the same species or between species (comparisons between the same sex) was tested by a non-analytic test (resampling F-test). The bootstrapped based tests calculate an F-score using the Procrustes Superimpostion. Then, we carried out to determine the probability that the observed F-value could have been generated by chance. To perform the bootstrapping procedure, the two groups wee pooled together. After that, two groups of equal sample size as the original data sets were drawn with repalacement form the common pool The distribution of bootstrapped F-values over 100 bootstrap data sets was used to determine the probability that the observed F-value could have arisen by chance.

The approach we have taken to comparing rates and timings of development and growth retains the meaning of the ALBERCH et al. (1979) parameters. Our approach accommodates both the curvilinearity of ontogenies in shape space and the nonlinearity of rates relative to time, minimizing dimensionality bias.

RESULTS

Growth curves using traditional measurements[24]- In *A. australis*, the number of measurements that presented correlations equal or higher that 0.85 in the females were three and in the males were ten (Table 3 and 4). The larger correlation with age was CPM in the females and CJU[25] in the males. Which revealed the higher percentual of explained variation was CPM for the females and CJU, for the males (Tables 3 and 4). The lower was LCC for the females and AFM for the males.

The metric characters presented different patterns in growth coefficient for males and females and the females seem more accelerated.

In the females, the measurement with higher rate was LCC (k=0.94) and DPS (k=0,39) (Table 3) and in the males were CPP and CRO (k=0.14) (Table 4). The females the stabilization at 95% of the curve of asymptotic growth of the variables obtained a high correlation (r≥0.85) in the Gompertz curve started at age 8 in CPM, at age 9 in CRO and at age 3 in LIM (Table 4). Considering that the mean of all variables reached at 95% with r ≥0.85 were at age 6, we considered than the females attain physical maturity of the skull at the age of 6 years old.

In males the stabilization at 95% of the curve of asymptotic growth started at age 4 in AJU, LON, DPS; in LRO were stabilized at age 7; CPP were stabilized at 12 years old; DBC and CJU were stabilized at

[24] Some variables like LCO, LCC, LBO, AFM (related with the known precocious developmental of the neural system) sometimes could not be described by the choiced growth models, resulting in error or redundance. When this was the case, the variable is excluded from our results.
[25] For the acronyms, see “Table of measurements” in the Appendix 1.

age 12; LIM and LZI were stabilized at age 14 and 16, finally CBH was stabilized at age 23. The mean the all variables with asymptotic growth at 95% and r ≥0.85 were at age 8. Therefore age of attainment of physical maturity of the males skull was estimated at 8 years old .

The results of the Student t-test of physically immature and physically mature skulls separately of *A. australis* , showed the presence of sexual dimorphism ($p<0.05$) for both age classes. In physically immature skulls eight variables were dimorphic: DBC, DPS, DCO, LCO, LMP, LRO and LZI . In physically mature skulls sixteen variables were sexually dimorphic: CBH, CCB, CJU, CPM, CPP, CRO, DBC, DCO, DPS, LBO, LMP, LRO and LZI.

Table 3. Parameters calculated by the Gompertz model in *Arctocephalus australis* females. A_∞ is asymptotic length in centimeters; *k* is the growth coefficient centimeters/year, t_0 is hypothetical age in which the species/sex would have had length equal zero (years); r is the correlation coefficient with age; PEV is the percentual of the variance explained and A_∞* 0.95 is when 95% of asymptotic length was achieved (in years); *t* is the unit of time measured in years when A_∞* 0.95 is attained (in years). The measurements which the correlations with the absolute age is higher than 0.85 are labeled by an asterisk (*) and the correlation value is in bold.

Acronyms	A_∞	K	t_0	R^2	PEV	A* 0.95	t
AJU	**2.70938626**	**0.32797083**	**-2.29715547**	**0.72925**	**53.18**	**2.20423171**	**-**
AOR	**5.19424549**	**0.27804411**	**-5.63136455**	**0.78225**	**61.19**	**2.57391695**	**-**
CBH	**18.9779213**	**0.27021467**	**-4.12479351**	**0.83424**	**69.60**	**4.93453321**	**-**
CCB	**21.1805992**	**0.26847815**	**-4.36157705**	**0.83834**	**70.28**	**18.0290253**	**-**
CJU	**8.13277457**	**0.26296396**	**-3.56056043**	**0.81462**	**66.36**	**20.1215692**	**-**
CPM*	**10.7630304**	**0.10515737**	**-10.535904**	**0.86441**	**74.72**	**7.72613584**	**8**
CPP	**8.98175724**	**0.30971994**	**-2.97713646**	**0.66720**	**44.520**	**10.2248789**	**-**
CRO*	**5.81824244**	**0.27452288**	**-3.5156834**	**0.88320**	**78.000**	**8.53266938**	**9**
CSP	**5.56338776**	**0.19749525**	**-5.98246524**	**0.81199**	**65.930**	**5.52733032**	**-**
DBC	8.36728672	0.24659867	-6.17866167	0.68543	46.980	5.28521837	-
DCM	7.24554112	0.26983534	-4.77147033	0.68794	47.330	7.94892239	-
DCO	4.83756136	0.30411465	-6.29897712	0.67409	45.440	6.88326406	-
DPS	4.28129069	0.39504172	-3.79515749	0.41438	17.170	4.59568329	-
LBO	3.41277051	0.27432272	-4.88766385	0.68295	46.640	4.06722615	-
LCC	7.27442074	0.93893819	-3.60577838	0.28826	8.310	3.24213198	-
LIM*	10.5809995	0.27875389	-3.35828826	**0.84666**	71.680	3.07406098	3
LMP	3.91955695	0.20847254	-6.99113198	0.48282	23.310	10.0519495	-
LON	2.8774463	0.19985518	-5.5823735	0.68218	46.540	3.7235791	-
LRO	3.79902152	0.29352232	-3.79297986	0.60999	37.210	2.73357399	-
LZI	12.4564089	0.21344622	-4.61525153	0.83564	69.830	3.60907044	-

Table 4. Parameters calculated by the Gompertz model in *Arctocephalus australis* males. A_∞ is asymptotic length in centimeters; *k* is the growth coefficient centimeters/year, t_0 is hypothetical age in which the species/sex would have had length equal zero (years); r is the correlation coefficient with age; PEV is the percentual of the variance explained and A_∞* 0.95 is when 95% of asymptotic length was achieved (in years); *t* is the unit of time measured in years when A_∞* 0.95 is attained (in years).

Acronyms	A_∞	K	t_0	R^2	PEV	A* 0.95	t
AFM	9.70612639	0.00755425	45.1301794	0.31571	9.970	9.22082007	-
AJU*	4.19118512	0.10801321	-1.19864687	0.85106	72.430	3.98162587	4
AOR	9.58431234	0.03651809	-5.98850565	0.72368	52.370	9.10509672	-
CBH*	23.7821564	0.13001012	-5.51866939	0.88637	78.570	22.5930486	23
CJU*	12.8263594	0.08495413	-2.36912455	0.90973	82.760	12.1850414	12
COM	13.9003871	0.09925406	-5.8956949	0.77723	60.410	13.2053678	-
CPP*	10.7653335	0.14454411	-4.49528635	0.86731	75.220	10.2270669	10
CRO	7.48695765	0.14251326	-3.7555731	0.81435	66.320	7.11260976	-
CSP	6.95711608	0.09358183	-7.4535453	0.75009	56.260	6.60926027	-
DBC*	12.2521699	0.07696164	-7.1958482	0.88785	78.830	11.6395614	12
DCM	12.0530169	0.04570177	-7.61206772	0.53492	28.610	11.450366	-
DCO	6.06711832	0.1638039	-6.35171032	0.55036	30.290	5.76376241	-
DPS*	7.25092923	0.08215838	-4.09865849	0.84768	71.860	6.88838277	7
LIM*	14.7360134	0.13682211	-3.07214936	0.90102	81.18	13.9992128	14
LMP	5.92282182	0.103628	-4.92710094	0.74413	55.37	5.62668073	-
LON*	7.34407767	0.04796542	3.95028466	**0.87606**	76.75	6.97687378	7
LRO*	7.04207026	0.08969911	-2.38412643	**0.88430**	78.20	6.68996674	7
LZI*	16.9535445	0.10651147	-4.28338035	**0.90743**	82.34	16.1058673	16

For *C. ursinus*, the number of measurements that presents correlations equal or higher than 0.85 in the females were fourtheen and in the males were five (Tables 5 and 6). That which presents the higher correlation with age is CBH in the females (Table 5) and CPP in the males (Table 6). That which shows the bigger percentual of explained variation was CBH (females) and CPP (males) and the lower was AFM for both sexes (tables 5 and 6). In regard of the growth coefficient, the metric characters presented different patterns for males and females. The females seem more accelerated. In the females, the measurement with higher rate was CPM (k=0.83) (Table 5) and in the males was LON (k=0.62) (Table 6).

The females the stabilization at 95% of the curve of asymptotic growth of the variables obtained a high correlation (r≥0.85) in the Gompertz curve started at age 3 in LBO and LON; LMP was at 4; CSP, DCO and LRO were at age 5; at age 6 were in AOR, CRO and DPS; at age 8 was DCM; CPP was at age 9; DBC and CJU were at age 10; LIM was at age 12 and CBH was at age 20 (Table 5). The mean of all variables reached at 95% with r ≥0.85 were at age 6, therefore we considered than the females attain physical maturity of the skull at the age of 6 years old.

In males the stabilization at 95% of the curve of asymptotic growth started at age 5 in CSP; CPP was stabilized at age 6; CJU was stabilized at 8; LZI was stabilized at 10; CBH was stabilized at age 16 and CCB was stabilized at age 18 (Table 6). The mean the all variables with asymptotic growth at 95% and r ≥0.85 was at age 8, therefore age of attainment of physical maturity of the males skull was estimated at 8 years old .

The results of the Student t-test of physically immature and physically mature skulls of *C. ursinus* separately, showed the presence of sexual dimorphism ($p<0.05$) for both age classes, respectively. In physically immature skulls were three variables dimorphic: AFM, LCO and LRO. In physically mature skulls twenty four variables were sexually dimorphic, only CSP, LCC and LCO were not dimorphic.

Table 5. Parameters calculated by the Gompertz model in females *Callorhinus ursinus*. A_∞ is asymptotic length in centimeters; *k* is the growth coefficient centimeters/year, t_0 is hypothetical age in which the species/sex would have had length equal zero (years); r is the correlation coefficient with age; PEV is the percentual of the variance explained and A_∞* 0.95 is when 95% of asymptotic length was achieved (in years); *t* is the unit of time measured in years when A_∞* 0.95 is attained (in years). The measurements which the correlations with the absolute age is higher than 0.85 are labeled by an asterisk (*) and the correlation value is in bold.

Acronyms	A_∞	K	t_0	r^2	PEV	A_∞* 0.95	t
AFM	3.0599741	0.06387125	-17.7914537	0.64076	41.06	2.9069754	-
AJU	3.64602122	0.12937922	-4.9875769	0.76848	59.06	3.46372016	-
AOR*	5.88055125	0.26744771	-3.60571137	**0.90737**	82.33	5.58652369	6
CBH*	20.9751958	0.34541667	-1.37864131	**0.98230**	96.49	19.926436	20
CJU*	10.8903752	0.29412552	-1.03428613	**0.95874**	91.92	10.3458565	10
CPM	11.8393104	0.83532431	-0.47084119	0.79942	63.91	11.2473449	-
CPP*	9.07984349	0.24745851	-1.31800577	**0.95735**	91.65	8.62585131	9
CRO*	5.81635574	0.37658822	-0.97285351	**0.96961**	94.02	5.52553795	6
CSP*	4.88209298	0.45953774	-2.00936032	**0.92366**	85.31	4.63798833	5
DBC*	10.0196781	0.15749852	-5.56322397	**0.95846**	91.86	9.51869421	10
DCM*	8.36461474	0.24641537	-2.86400943	**0.93716**	87.83	7.94638401	8
DCO*	5.45237891	0.40259611	-2.63204349	**0.88661**	78.61	5.17975997	5
DPS*	6.3355718	0.10887391	-5.03210525	**0.89558**	80.21	6.01879321	6
LBO*	3.5434312	0.59340385	-1.90911778	**0.91000**	82.81	3.36625964	3
LIM	12.2569586	0.24970159	-2.35925938	**0.95741**	91.66	11.6441107	12
LMP*	4.49538478	0.21416107	-1.98107398	**0.90815**	82.47	4.27061554	4
LON*	3.47999154	0.252706	-1.58972774	**0.96940**	93.97	3.30599196	3
LRO*	4.92466655	0.24551711	-1.39731038	**0.97050**	94.19	4.67843322	5
LZI	15.2895369	0.11981376	-5.75253967	0.81505	66.43	14.5250601	-

Table 6. Parameters calculated by the Gompertz model in males *Callorhinus ursinus*. A is asymptotic length in centimeters; k is the growth coefficient centimeters/year, t0 is hypothetical age in which the species/sex would have had length equal zero (years); r is the correlation coefficient with age; PEV is the percentual of the variance explained and A(* 0.95 is when 95% of asymptotic length was achieved (in years); t is the unit of time measured in years when A(* 0.95 is attained (in years). The measurements which the correlations with the absolute age is higher than 0.85 are labeled by an asterisk (*) and the correlation value is in bold.

Acronyms	A	k	t0	r^2	PEV	A(* 0.95	t
AJU	2.63197262	0.40223375	-4.60958851	0.39656	15.730	2.50037399	-
AOR	4.91617047	0.35030074	-6.35663011	0.59695	35.64	4.67036194	-
CBH*	17.0267515	0.52569996	-2.33200018	0.89878	80.78	16.1754139	16
CCB*	18.6712744	0.44515574	-3.04778953	0.86463	74.76	17.7377106	18
CJU	8.14862252	0.38423704	-3.13718725	0.84951	72.17	7.7411914	8
CPM	10.3931704	0.54420233	-2.70495613	0.74773	55.91	9.87351186	-
CPP*	6.71716691	0.47154641	-1.94204383	0.93924	88.22	6.38130856	6
CRO	4.79205089	0.22637415	-5.43708253	0.63419	40.22	4.55244834	-
CSP*	4.78329064	0.24659117	-4.82491442	0.88667	78.62	4.54412611	5
DBC	7.4438501	0.47791404	-4.31926642	0.77374	59.87	7.0716576	-
DCO	4.61511466	0.54337886	-3.81904614	0.72540	52.62	4.38435893	-
DPS	4.18480388	0.11605097	-12.4505253	0.59162	35.00	3.97556368	-
LBO	4.18480388	0.11605097	-12.4505253	0.59162	35.00	3.97556368	-
LIM	9.16470937	0.50610654	-3.44612579	0.67723	45.86	8.7064739	-
LON	2.38010703	0.62422188	-2.31657796	0.69758	48.66	2.26110167	-
LRO	12.6516508	0.02080811	22.9361661	0.77795	60.52	12.0190683	-
LZI*	10.8562331	0.35924866	-3.93745929	0.85628	73.32	10.3134214	10

About *O. byronia*, the number of measurements that presents correlations equal or higher that 0.85 in the females were ten and in the males were eleven (Tables 7 and 8). The variable with larger correlation coefficients obtained for *O. byronia* was CJU in the females (Table 7) and CCB in the males (Table 8). We denote that the higher percentual of explained variation was presented by CJU (females) and CCB (males) and the lower was and AFM for females and DCO for the males. In regard of the growth coefficient, females seem more accelerated. In the females, the measurement with higher rate was LCC (k=0.61) (Table 7) and in the males was CPP (k=0.31) (Table 8).

The results of the Student t-test of physically immature and physically mature skulls separately, showed the presence of sexual dimorphism ($p<0.05$) for both age classes. In regard of the growth coefficient, the metric characters presented different patterns for males and females. The females seem more accelerated, the measurement with higher rate was LCC (k=0.61) and DCO (k=0.53) (Table 7) and in the males was CPP (k=0.31) and CCB (k=0.28) (Table 8).

For the females the stabilization at 95% of the curve of asymptotic growth of the variables obtained a high correlation ($r\geq0.85$) in the Gompertz curve started at age 6 in AJU; LRO and CSP; CRO was at 7; DCM was at age 9; DBC and CJU were at age 10; LIM was at age 12; CPP was at age 14 and CCB was at age 24 (Table 7). The mean of all variables reached at 95% with $r \geq0.85$ were at age 9, therefore we considered than the females attain physical maturity of the skull at the age of 9 years old.

In males the stabilization at 95% of the curve of asymptotic growth started at age 5 in LON; AJU was stabilized at age 6; LMP and CRO were stabilized at 9; LRO was stabilized at 10; DPS and DCM were stabilized at age 12; CCB and CJU were stabilized at 13; DBC was stabilized at 16; LZI was stabilized at 21; CBH was stabilized at 30 and CCB was stabilized at 32 (Table 8). The mean the all variables with asymptotic growth at 95% and $r \geq0.85$ was at age 10, therefore age of attainment of physical maturity of the males skull was estimated at 10 years old.

The results of the Student t-test of physically immature and physically mature skulls separately, showed the presence of sexual dimorphism ($p<0.05$) for both age classes. In physically immature skulls, twenty one variables were dimorphic. Only CPP was non-dimorphic ($p>0.05$). In physically mature skulls all measurements were dimorphic ($p<0.05$).

Table 7. Parameters calculated by the Gompertz model in females *Otaria byronia* A_∞ is asymptotic length in centimeters; *k* is the growth coefficient centimeters/year, t_0 is hypothetical age in which the species/sex would have had length equal zero (years); r is the correlation coefficient with age; PEV is the percentual of the variance explained and A_∞* 0.95 is when 95% of asymptotic length was achieved (in years); *t* is the unit of time measured in years when A_∞* 0.95 is attained (in years). The measurements which the correlations with the absolute age is higher than 0.85 are labeled by an asterisk (*) and the correlation value is in bold.

Acronyms	A	k	t0	R	PEV	A(* 0.95	t
AJU*	3.71429229	0.24339258	-2.30646499	0.84613	71.59	3.52857768	6
AOR	5.95198389	0.46485688	-2.44965398	0.74600	55.65	5.65438469	-
CBH	23.2556113	0.34479511	-1.97338443	0.76496	58.52	22.0928307	-
CCB*	26.0183701	0.36520847	-2.36025764	0.87053	75.78	24.7174516	-
CJU*	10.0913292	0.26496673	-2.16361539	0.91308	83.37	9.58676274	10
CPM	8.82895514	0.310294	-4.02954671	0.77641	60.28	8.38750739	-
CPP*	14.9604855	0.33890283	-1.59910478	0.89177	79.53	14.2124612	14
CRO*	7.164109	0.26677143	-2.43114115	0.89648	80.37	6.80590355	7
CSP*	6.69324668	0.29972983	-3.51273224	0.85926	73.83	6.35858435	6
DBC*	10.6058441	0.28399894	-4.87349102	**0.85918**	73.82	10.0755519	10
DCM*	8.96896467	0.27121622	-4.52268603	**0.85828**	73.66	8.52051644	9
DCO	5.75166514	0.52618195	-3.2940196	0.76415	58.39	5.46408189	-
DPS	8.14590093	0.18357288	-4.19213213	0.83281	69.36	7.73860589	-
LBO	4.51166077	0.30810414	-3.90438543	0.79713	63.54	4.28607773	-
LCC	8.03999091	0.61313999	-4.52732385	0.42242	17.84	7.63799137	-
LIM*	12.7144042	0.31985345	-3.56521683	**0.85209**	72.61	12.078684	12
LMP	5.97467306	0.19556679	-4.64818697	0.81433	66.31	5.67593941	-
LON	3.59842322	0.36153549	-3.10427453	0.82714	68.42	3.41850205	-
LRO*	5.94455962	0.29803804	-2.69251453	**0.89404**	79.93	5.64733164	6
LZI	14.9962267	0.26450832	-3.41768104	0.81053	65.70	14.2464153	-

Table 8. Parameters calculated by the Gompertz model in males Otaria byronia A(is asymptotic length in centimeters; k is the growth coefficient centimeters/year, t0 is hypothetical age in which the species/sex would have had length equal zero (years); r is the correlation coefficient with age; PEV is the percentual of the variance explained and A(* 0.95 is when 95% of asymptotic length was achieved (in years); t is the unit of time measured in years when A(* 0.95 is attained (in years). The measurements which the correlations with the absolute age is higher than 0.85 are labeled by an asterisk (*) and the correlation value is in bold.

Acronyms	A(	k	t0	r	PEV	A* 0.95	t
AJU*	6.124890403	0.23066747	0.39886397	**0.90797**	82.44	5.81864588	6
CBH	31.65141551	0.23842315	-1.37859119	0.83562	69.83	30.0688447	32
CCB*	34.23702899	0.27733332	-1.5397922	**0.94083**	88.52	32.5251775	13
CJU*	13.83992437	0.21424282	-0.81434814	**0.93047**	86.58	13.1479281	-
CPP	18.43920884	0.31349614	-1.02079291	0.67990	46.23	17.5172484	-
CRO*	9.964393839	0.26956967	-1.0101195	**0.87408**	76.40	9.46617415	9
DBC*	16.95133429	0.18261528	-1.88776772	**0.90975**	82.76	16.1037676	16
DCM*	13.33432893	0.19750435	-2.09286889	**0.92237**	85.08	12.6676125	12
DCO*	6.989518137	0.28753494	-4.23455409	**0.83266**	69.33	6.64004223	-
DPS*	13.46240501	0.19689447	-0.33887856	**0.92339**	85.27	12.7892848	12
LCC	9.219700682	0.17336579	-10.5500701	0.63045	39.75	8.75871565	-
LIM	19.69047015	0.19961408	-1.48911088	0.82161	67.50	18.7059466	-
LMP*	9.049815696	0.24196929	-1.01058683	**090168**	81.30	8.59732491	9
LON	5.522879235	0.22514058	-1.51487803	0.87246	76.12	5.24673527	5
LRO*	10.8626549	0.23866847	-0.04246777	**0.89662**	80.39	10.3195222	10
LZI*	22.06055487	0.21070472	-1.27961839	**0.86497**	74.82	20.9575271	21

Rates and timings of developmental and growth using Geometric Morphometrics techniques-

Some models were excluded because they presented auto-correlations among residuals in one or more of the analyses (Table 9). Of those that remained, several fitted equally well. We chose the linear model as the basis for comparing rates and timings of growth and development because it is simple and fits both the developmental and growth data well in all species/sex groups. Furthermore, the AIC weight is largely greater in this model in comparison with all the others, in all cases.

Table 9. Relative fit of the eight models fitted to the measure of developmental maturity. The AIC weight evaluates relative goodness-of-fit by balancing the distance between model and data by degrees of freedom. AC refers to serial autocorrelations among residuals of the model. The model in bold is the one judges best. NS=not significant, S=significant.

SPECIES/SEX	MODEL	AIC WEIGHT	AC	%VARIANCE
A. australis (females)	Monomolecular	0.1390	NS	50.1742
	German Gompertz	0.1438	NS	51.8306
	Logistic	0.1429	NS	51.5325
	Quadratic	0.1400	NS	50.5146
	LINEAR	**0.3780**	**NS**	**50.1855**
A. australis (males)	Chapman -Richards	0.0716	NS	90.4128
	Monomolecular	0.0778	NS	76.0174
	Von Bertalanfly	0.1201	NS	84.4614
	Gompertz	0.0886	NS	78.9462
	German Gompertz	0.1607	S	88.3888
	Logistic	0.1710	NS	89.0890
	Quadratic	0.0984	NS	81.0389
	LINEAR	**0.2117**	**NS**	**76.0375**
C. ursinus (females)	Monomolecular	0.1433	NS	58.0295
	German Gompertz	0.1469	S	59.0461
	Logistic	0.1450	NS	58.5172
	Quadratic	0.1434	S	58.0581
	LINEAR	**0.3870**	**NS**	**57.7521**
C. ursinus (males)	Chapman -Richards	0.0532	NS	59.0048
	Monomolecular	0.0993	NS	40.3318
	Von Bertalanfly	0.1297	NS	54.3311
	German Gompertz	0.1406	NS	57.8616
	Logistic	0.1445	NS	58.9925
	Quadratic	0.1628	NS	63.6036
	LINEAR	**0.2700**	**NS**	**40.3583**
O. byronia (females)	Chapman -Richards	0.0443	NS	47.0284
	Monomolecular	0.1091	NS	41.5193
	Von Bertalanfly	0.1129	NS	43.5221
	Gompertz	0.1119	NS	43.0260
	German Gompertz	0.1131	NS	43.6124
	Logistic	0.1136	NS	43.8770
	Quadratic	0.1116	NS	42.8454
	LINEAR	**0.2834**	**NS**	**38.8225**
O. byronia (males)	Chapman -Richards	0.0473	NS	65.0136
	Monomolecular	0.1103	NS	59.2314
	Von Bertalanfly	0.1143	NS	60.6415
	Gompertz	0.0850	NS	47.0971
	German Gompertz	0.1145	NS	60.7151
	Logistic	0.1151	NS	60.9288
	Quadratic	0.1134	NS	60.3278
	LINEAR	**0.3001**	**NS**	**59.2544**

Table 10. Relative fit of the eight models fitted to the Logaritm Centroid Size. The AIC weight evaluates relative goodness –of-fit by balancing the distance between model and data by degrees of freedom. AC refers to serial autocorrelations among residuals of the model. The model judged best is in bold type. NS=not significant, S=significant.

SPECIES/SEX	MODEL	AIC WEIGHT	AC	%VARIANCE
A. australis (females)	Chapman -Richards	0.0590	NS	80.0310
	Monomolecular	0.0981	NS	67.3566
	Von Bertalanfly	0.1192	NS	73.1465
	Gompertz	0.1012	NS	68.3620
	German Gompertz	0.0940	NS	65.9332
	Logistic	0.1590	NS	79.8682
	Quadratic	0.1024	NS	68.7314
	LINEAR	**0.2672**	**NS**	**67.4325**
A. australis (males)	Chapman -Richards	0.0557	NS	91.6098
	Monomolecular	0.1064	NS	88.0632
	Von Bertalanfly	0.1269	NS	89.9919
	Gompertz	0.0472	S	73.1099
	German Gompertz	0.1167	NS	89.1233
	Logistic	0.1419	NS	91.0511
	Quadratic	0.1146	NS	88.9255
	LINEAR	**0.2906**	**NS**	**51.4160**
C. ursinus (females)	Chapman -Richards	0.0159	NS	0.0000
	Monomolecular	0.1257	NS	65.6536
	Von Bertalanfly	0.0432	NS	0.0000
	Gompertz	0.0432	NS	0.0000
	German Gompertz	0.1428	NS	69.7586
	Logistic	0.1411	NS	69.3969
	Quadratic	0.1457	NS	70.3746
	LINEAR	**0.3425**	**S**	**65.7318**
C. ursinus (males)	Chapman -Richards	0.0480	NS	39.7206
	Monomolecular	0.1180	NS	33.3372
	Von Bertalanfly	37.2402	NS	0.1254
	German Gompertz	0.1281	NS	38.5667
	Logistic	0.1305	NS	39.6977
	Quadratic	0.1289	NS	38.9464
	LINEAR	**0.3211**	**NS**	**33.3953**
O. byronia (females)	Monomolecular	0.0905	NS	43.6617
	Von Bertalanfly	0.0990	NS	48.5272
	Gompertz	0.0888	NS	42.6058
	German Gompertz	0.1001	NS	49.0710
	Logistic	0.1121	NS	54.5346
	Quadratic	0.0936	NS	45.5658
	LINEAR	**0.2461**	**NS**	**43.6875**
O. byronia (males)	Chapman -Richards	0.0153	NS	0.0000
	Monomolecular	0.1232	NS	66.1830
	Von Bertalanfly	0.0417	NS	0.0000
	Gompertz	0.0417	NS	0.0000
	German Gompertz	0.1467	NS	71.5894
	Logistic	0.1479	NS	71.8307
	Quadratic	0.1481	NS	71.8626
	LINEAR	**0.3354**	**NS**	**66.2215**

Only *O. byronia* differ between sexes in both developmental model parameters (constant and slope). It is striking yet the major linearity of the females of this species, which can be perceive regarding the difference between the percentile of explained variation explained by the linear model between the sexes of this species (and in which concerns that point, in *A. australis* too). In contrast, *A. australis* and *C. ursinus* do not reveal differences between sexes in which concerns the relationship between changes in shape and absolute age (Table 11).

Table 11. Developmental rate for each species/sex examined using the linear model. Confidence intervals (95%) are between parentheses.

		Constant	Slope
A. australis	**females**	-4.787 (-3.821 -> -4.845)	141.280(129.241-> 146.078)
	males	-4.577 (-3.693 -> -4.862)	147.411(136.985-> 149.385)
C. ursinus	**females**	-2.837 (1.679 -> -3.640)	87.467 (33.777 -> 96.462)
	males	-1.787 (-4.032 -> -2.940)	72.341 (113.182 -> 65.194)
O. byronia	**females**	-8.103 (-9.662 -> -15.498)	111.510(110.702-> 164.954)
	males	-3.919 (-4.228 -> -3.239)	81.089 (75.360 -> 83.538)

The rate of growth in *A. australis* is not different between the sexes (and either for the constant) but is higher than the rate of the other species, especially in comparison with *C. ursinus*. The other two species present rates significantly different between sexes in which concern growth (and in the constant too) (Table 12).

Table 12. Growth rate for each species/sex examined using the linear model. Confidence intervals are between parentheses.

		Constant	Slope
A. australis	**females**	-82.700(-77.071-> -85.503)	25.725 (23.905 -> 23.609)
	males	-81.758 (-91.696->-65.032)	25.472(28.495 -> 20.240)
C. ursinus	**females**	-35.421(-44.222-> -31.941)	11.439 (14.175 -> 10.574)
	males	-17.022 (-2.433 -> -26.420)	5.759 (1.363 -> 8.627)
O. byronia	**females**	-28.068(-30.047-> -19.960)	9.666 (10.159 -> 7.149)
	males	-44.099(-45.133-> -47.915)	13.364 (13.525 -> 14.271)

Using geometric morphometrics data sets, the comparisons between the growth and developmental models in different species result always significantly different in both parameters (slope and constant). The differences between species are more remarkable between the males that between females for both, developmental and growth trajectories.

We were not able to evaluate the relative grade of shape and size for each age (proportion of the maturity/size of the adult attained in each age in each group of species/sex) because our range of ages sampled do not permit to determine the point of stabilization of development or growth. For the same reason, it was not possible to determine the time of development and growth in each species/sex group (in which age the ontogeny stabilize) using the geometric data sets.

That limitation could not be solved by the employment of sutural ages because any model have a good fit to this kind of data (which means that the percentile of explained variation is very small or not greater that could be access by chance). This is especially true for the females of the fur seals, where the ontogenetic changes are less conspicuous.

DISCUSSION

Most morphological changes during an organism's ontogeny occurs during the juvenile phase of growth, particularly during early juvenile development. A relevant characteristic of the sigmoidal models is that growth rates decay over time (which indicate that the ratios of specific growth rates vary thorough ontogeny). All measurements follow the same growth curve; their differing values of k tell us how they are displaced relative to each other in time—different parts of the skull reach the same point on their growth curves at different times. And considering that growth rates decay over time, a more negatively allometric part has decayed over a longer time probably because it began growing earlier, as sometimes is the case of the size of the orbit in our analysis of the linear measurements.

The choice of the linear model for the geometric datasets could be related/explained if we consider that perhaps the sample do not include sufficiently young animals to represent the sigmoidal part of the growth curves, or yet due to the sample size.

The physical maturity observed for the specimens of *A. australis* are congruent with the SCHILLER (2000) results. Interestingly, the fur seals of both species mature at similar ages (females and males) but *O. byronia* presents a larger time of growth, whitch is congruent with a longer ontogenetic trajectory[26]. The growth results are congruent with the results presented for the 3 species by BRUNNER (2000), employing sutural ages like a measurement of age and Von Bertallanfy model to describe the growth.

The percent of the explained variance by the model is congruent, in general, with the correlation of the measurements with absolute age. The measurements with a very low percent of explained variation (e. g. LCC, AFM, LCO) are precocious measurements (accelerated) and related to the neural system, which obviously develops in the early ontogeny. Other measurements with low percentile of explained variance and/or correlation of age are the post-caninal length measurements, which is in agree with the factdefinitive dentition erupt in the first year of life in otarids (BERTA & SUMICH, 1999). These results are congruent with the allometric pattern of this variable (anterior chapter).

The variables that are dimorphic between the imatures are approximatelly the same between the fur seals (and the majority are related with the braincase and neighborhood). By contrast, sexual dimorphism is more strong and ample in the imatures of *O. byronia*, which perhaps is linked with body size at birth. Additionally, all linear measurements are dimorphic in the adults of the later species.

SCHILLER (2000) had detect sexual dimorphism in all linear measurements of the syncranium of *A. australis* of imatures and adults specimens (except for LON in the juveniles). Those differences are surely due to the different samples sizes and techniques of determination of age, more robust in SCHILLER´s research.

Males show a significantly steeper slopes than females indicating a dissociation of size and shape. By contrast, departures from ontogenetic scaling, where size and shape are dissociated with adult males being disproportionately larger than adult females, are found in cranial regions associated with secondary sexual character development (LEUTENEGGER & MASTERSON, 1989b).

With respect to the sexual dimorphism, it is important to contextualize the differences here described in that most pinniped males do not become "socially mature" until several years (usually at least 3-4 years) after reaching sexual maturity. Although a young male may be capable of breeding at a certain age, he is

[26] Interesting in that context is the slower rate of development of the males in relation with that of the females.

rarely able to copulate successfully with a female or to compete effectively with the dominant or territorial bull until he is older (RIEDMAN, 1990). In that context, is attempted that sexual dimorphism level increase during ontogeny and that it will be more conspicuous and generalized in the adults, were secondary dimorphism develops too (structures related with muscles like the temporal or the masseteric; size of canines and other ones related to robustness).

In most pinnipeds the females attained the reproductive age much earlier than males, spending a lot of energy on their offspring and thus their ability for further somatic growth is limited. In contrast, males do not provide parental care and in most cases reach maturity later in life. They can allocate more energy to growth and hence male pinnipeds often show a dramatic secondary growth spurt during their adolescent years. LINDENFORS et al (2002) do not found a significant relationship between body size and sexual size dimorphism in pinnipeds and their points then, that sexual size dimorphism in pinnipeds is a result of selection working on males alone.

Whereas the evolution of genetically based sexual size dimorphism in adults is extremely slow, there is a rapid evolution of differences between males and females in growth patterns, and these differences evolve not just among related species. This is perfectly illustrated by long-growing species in which selection on males and females during growth, and not during the adult stage, is the most important determinant of adult SSD (LEIGH, 1995). Moreover, the need for within-organism integration during prolonged and complex development might determine the aspects of variation available to selection (ARTHUR, 2002); thus, the internal dynamics of the developmental program that is shared between the sexes might have a profound influence on the evolution of sexual size dimorphism.

According to recently developed sex-ratio theories, a parent should vary the amount of maternal investment in relation to its offspring´s sex by investing more in the sex with the highest variance in reproductive success (in our case, the males) since parental investment influences the offspring´s body size, health, and breeding success later in life (MAYNARD SMITH, 1980). In fact, male otarid pups frequently weighed more at birth, grew at a faster rate, or ingested more milk than female pups during the lactation period (MATTLIN, 1981; DOIDGE et al. 1984; BONESS et al., 1985; KOVACS & LAVIGNE, 1986; COSTA & GENTRE, 1986; TRILLMICH, 1986; HIGGINS et al. 1988).

The two different approaches presented here reveals different results in which concerns sexual dimorphism, but we have to maintain in mind that the geometric analyses treat the skull as simple structure and the approach using the linear measurements implies a certain “modularity”. But unfortunately, integration and modularity in otarids skull are, until the present, a completely unexplored territory.

Numerous times ontogenetic scaling is presented in the literature to explain sexual dimorphism (e. g. LEUTENEGGER & LARSON, 1985). Following these approaches, shape differences between the adult males and females result from the extension of relative growth (shape change) in the smaller females to larger overall size in the males (SHEA, 1986). Equally common are the examples where females reach their adolescent growth spurt, attain sexual maturity, and cease growth before males do (TANNER, 1962). Thus, from a perspective of heterochrony, the null hypothesis predicts that adult sexual dimorphism in size and shape is primarily the result of time hypermorphosis, i. e. an extension of the growth period in time in males (SHEA, 1986). But that is surely a scenario related with dimensionaly bias.

In that context, in which concerns the geometric analysis of the fur seals, it seems that rates or timings of growth and development evolve below a conserved spatiotemporal organization of morphogenesis. But channeling can occur when growth and development are associated (ontogenetic

scaling) or decoupled (exclusively changes in rate that are consistent with the hypothesis that morphogenesis is conserved are verified[27]), which could be the case of the evolution of sexual dimorphism in *A. australis* and *C. ursinus*, respectively. The major similarity between the fur seals species is coherent with the fact that closely related organisms grow at similar rates relative to their size, even when size is variable (WAYNE, 1986).

It was suggest in the specialized literature (e. g. MASTERSON & LEUTENEGGER, 1989; McKINNEY & McNAMARA, 1991) that the combination of data on cranial growth allometries and sex differences in developmental timing offers insights as to the kind of heterochronic processes that may lead to specific patterns of adult cranial sexual dimorphism, like peramorphic males where they growing for a longer period of time than females ("time hypermorphosis").

It is true that, once a time channeling is found, and age data are available (or collected) it will be possible to go further and identify the changes in developmental rate and/or timing appling GOULD (1977) and ALBERCH et al. (1979) formalisms. But we could not conclude about that subject because our age samples do not provide information about the length of the ontogenetic trajectory (stabilization of development and growth).

Finally in future studies, it will be interesting asking whether skull shape maturity predicts the timing of life-history.

[27] We expect the "descendant" ontogeny to be more nearly isometric than the "ancestor's". One example is when positively allometric coefficients will *decrease* in slope whereas negatively allometric coefficients *increase* because positively and negatively allometric coefficients approach isometry from opposing directions.

Appendix1. List of the acronyms with the descriptions of the linear measurements.

Acronyms	
AFM	MAXIMUM OF HEIGHT OF THE *FORAMEN MAGNUM*
AJU	MAXIMUM HEIGHT OF THE JUGAL
AOR	MAXIMUM WIDTH ORBIT
CBH	BASILAR HENSEL LENGTH
CCB	BASAL-CONDYLE LENGTH
CJU	LENGTH OF THE JUGAL
CPM	DISTANCE BETWEEN THE PALATE AND THE *FORAMEN MAGNUM*
CPP	PALATE LENGTH
CRO	ROSTRUM LENGTH
CSP	POS-CANINE SERIES LENGTH
DBC	DISTANCE BETWEEN THE TYMPANIC BULE AND THE SAGITAL CRIST
DOM	DISTANCE BETWEEN THE OPTICAL *FORAME* AND THE *FORAMEN MAGNUM*
DCO	MAXIMUM DISTANCE BETWEEN THE CONDYLES
DPS	MAXIMUM DISTANCES BETWEEN THE SUPER-ORBITAL PROCESS
LBO	BASIOCCIPITAL WIDTH
LCC	MAXIMUM WIDTH OF THE BRAINCASE
LCO	MINIMUM WIDTH AT THE INTER-ORBITAL CONSTRICTION
LIM	MAXIMUM WIDTH BETWEEN THE MASTOID PROCESS
LMP	MAXIMUM WIDTH OF THE PALATE
LON	MAXIMUM WIDTH OF THE NASAL ORIFICE
LRO	MAXIMUM ROSTRUM WIDTH
LZI	MAXIMUM WIDTH OF THE ZYGOMATIC ARCH

APENDIX 2. ANATOMICAL DESCRIPTION OF THE LANDMARKS

1- anteriormost point of the pré-maxilla tuberosity
2- antero-lateral extremity of third incisive alveolus
3- anteriormost point of incisive foramen
4- lateral extremity of canine alveolus
5- anteromedial point of first post-canine alveolus
6- anteriormost point of the maxilla-palatine suture
7- point that label the direction change of the maxilla-palatine suture
8- posteriormost point of the root at the lateral limit at bone palate of zigomatic process of the maxilla
9- posteriormost point of sixth post-canine alveolus
10- posteriormost point of palatine extension of maxilla (“pterygoid” process of the maxilla)
11- posteriormost point of interpalatine suture
12- point that label the direction change of the posterior border of palatine
13- posteriormost extremity of oval foramen
14- lateral extremity of jugal-esquamosal suture
15- medial extremity of the contact between the glenoid fossa and the ectotympanic
16- anteriormost extremity of the anterior aperture of carotid canal
17- antero-lateral corner of mastoid process
18- posteriormost point of the condiloid foramen
19- posteriormost point of occipital condyle
20- anteriormost point of foramen magnum.

CAPÍTULO III

COMPARATIVE DESCRIPTION OF DIMORPHISM IN SKULL ONTOGENIES OF *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia* (PINNIPEDIA: OTARIIDAE)

COMPARED DESCRIPTION OF DIMORPHISM IN SKULL ONTOGENIES OF *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia* (PINNIPEDIA: OTARIIDAE)

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ABSTRACT

The ontogeny has a relevant role on the sexual dimorphism pattern, extreme in the otarids, but is yet somewhat obscure in the majority of taxa. We focus here on *Arctocephlaus australis*, *Callorhinus ursinus* and *Otaria byronia* ontogenies that with the aim of contributing to the understanding of the origin, structure and temporal patterns of otarid morphological diversity. Our aims are: to compare the skull ontogeny of the species invocated in identifying and in describing shape alterations in the skull; to evaluate and to describe comparatively the sexual dimorphism during the ontogeny and to study the covariance between size and shape in relationship with age-groups. The pattern of change in shape during postnatal development in otarid skull was studied and described by geometric morphometric techniques including comparisons between mean shapes, multivariate regression and comparisons of allometric vectors, disparity levels among other techniques. The dimorphism is more conspicuous in adult shapes but this is not true for the level of disparity between sexes of *O. byronia*. Although the dimorphism is linked with size this is not only a question of allometry (which is present in the morphogenesis of all species, especially in *O. byronia*). Additionally, the slopes of changes in shape related with size increase are different between sexes in *A. australis* and *O. byronia*, but are equal in *C. ursinus*, which is the smaller species. We could have suggest post-displacement like one of the factors that could acted in the origin of the sexual dimorphism in the skull of *C. ursinus,* but age information is needed for that. Heterochrony, perhaps is present in the roots of the modifications suffered by the ontogeny of males and females of*A. australis* and *O. byronia* too, considering the differences in the rates of development between the sexes of both species (and overall in *O. byronia*), but surely repatterning allometry is involved too in these cases.

INTRODUCTION

Pinnipedia contains some of the most spectacular examples of sexual size dimorphism, examples that are therefore frequently used to illustrate the theory of sexual selection (LINDERFORS et al., 2002). Understanding the developmental, structural and functional organization of animals is one important aim of organismal biology, particularly of comparative morphology. In addition, hard modifications in skull morphology are many times related not only with life conditions and specifically necessities, but with the ontogenetically process too. The ontogenetical studies may determine if an intense shape modification is or not related with selection for size or particular ecological contexts, for instance. It contributes for the functional biology and to the knowledge of adaptation of specific regions of the body and is crucial for the elaboration of an epigenetically and/or canalization based approach, when variance can be adequately controlled.

A number of authors have recently stressed the importance of elucidating the ontogenetic basis of sexual differences in adult morphology as a means to understanding how patterns of sexual dimorphism relate to social, ecological, and nutritional factors. In particular, JARMAN (1983) has noted that similar patterns of adult dimorphism may be achieved via diverse ontogenetic pathways, and variation among these may reflect fundamental differences in social structure or ecological factors. SHEA (1986) generalized these issues in terms of heterochrony and the parameters of size, shape, and timing, and applied this analysis to selected cases of sexual dimorphism among anthropoid primates.

Shape contrasts between sexes are closely linked to size differences besides the fact that variance dimorphism appears to be relatively independent of size effects. There are differences in their magnitudes and patterns of sexual shape contrasts. Some authors suggested that the differences which occur between groups in their patterns of sexual dimorphism are probably the result of a mixture of time and rate acting upon different ontogenetic trajectories (O´HIGGINS et al. 1990). They also demonstrate that there are differences in their magnitudes and patterns of sexual shape contrasts.

Initiation and continued existence of marked sexual dimorphism and associated polygyny requires that females stay together, which is the case in Otariidae. This gives some males the potential to increase mating success, and fosters male intrasexual competition. Hence larger body size and canine size are favored in males but not in females, leading to dimorphism (HAMILTON, 1977).

We focus here on *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia* with the aim of contributing to the understanding of the origin, structure and temporal patterns of otarid morphological diversity.

We present a comparative study of the ontogeny of the skull of the two Otariidae species more frequent in the coast of Rio Grande do Sul State, Brazil (*O. byronia* and *A. australis*). *Callorhinus ursinus* is also included because it is supposely the extant otarid more closely related to the ancestral of this family. In this context, its analysis could collaborate with the systematic of Otariidae and with the understanding of the evolutionary mechanisms that acted in the focused taxa. There is a large literature about the sexual dimorphism in otarid, including the species studied here (e. g. CHIASSON, 1957; CRESPO, 1984; 1988; DREHMER, 1997; SANFELICE, 1999) but the ontogeny of the dimorphism is yet obscure.

The ontogeny has a relevant role on the sexual dimorphism pattern, extreme in the otarids. Studies of growth gradients are particularly successful in describing the ontogeny of sexual dimorphism, which is extreme in the otarids. (e. g. Allometrical patterns that promote alterations in the proportions may be adaptations that maximize the physiological and ecological efficiency, that have as consequence the modification of the possible size to attain during the ontogeny and phylogeny,) (GOULD, 1965).

In this context, our specific objectives are: (1) to investigate comparatively the skull ontogeny of the species infocated in identifying and in describing shape alterations in the skull (and/or in the relations of the different structures too) during the ontogeny of the three species infocated; (2) to evaluate and to describe comparatively the sexual dimorphism during the ontogeny in size and shape; (3) to study the covariance between the size and shape in relationship with age-groups.

In summary, we hope to compare the groups/sexes asking how particular causes affect shape similarly or differently. It means that we want to test the hypothesis that the magnitude of the effect is the same in all groups, and that the particular responses (i.e., its effects on shape) are the same in all them.

MATERIAL AND METHODS

Data- Our sample comprise a cross-sectional ontogenetic series of skull of three otarid species: *A. australis* (n=76), *C. ursinus* (n=51) and *O. byronia* (n=84).

The sample numbers, size ranges found, and maximum size observed in this study are presented below (Table 1).

Table 1. Caracterization of the studied sample. Size is presented in units of centroid size.

	SAMPLE NUMBERS	SIZE RANGES OBSERVED IN UNITS OF CENTROID SIZE
Arctocephalus australis	76	18.9332 - 43.948
Callorhinus ursinus	51	21.0265 - 46.9817
Otaria byronia	84	14.8127 – 57.6586

We use the sutural ages to determine the ontogenetic stages (SIVERTSEN, 1964). The analyses were performed considering species, sex, sutural age groups (juveniles, subadults and adults).

The analyses of ontogenetic change in morphology are based on landmarks, discrete points that are recognizable and biologically correpsondent on all specimens in the study (Fig. 1). These landmarks can be localized and are common to inall species and ontogenetic stages. They were selected to provide the most comprehensive and even coverage possible. Furthermore, consistency of relative position, repeatability and coplanarity of the landmarks were taken account in the choice of the landmarks points.

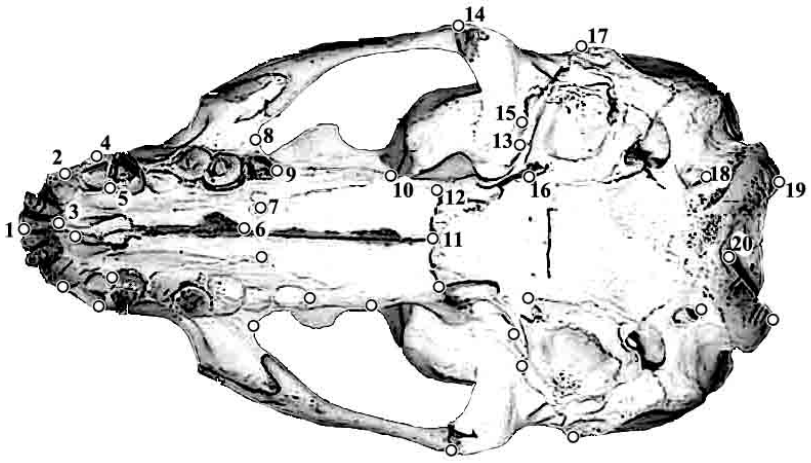

Figure 1. Landmarks shown on the ventral view skull of a juvenile of *Otaria byronia*. Descriptions of each landmark are given in Appendix 1.

The skulls were photographed in ventral view with the palate oriented parallel to the photographic plane, and digitalized on both right and left sides. All landmarks were digitized on the ventral view of the skull by one person (D. Sanfelice). Bilaterally homologous landmarks were averaged to avoid inflating degrees of freedom, but the results are depicted for whole skulls to facilitate the comprehension. The landmarks are digitalized in TpsDig (ROHLF, 1998), which is freeware distributed at http://life.bio.sunysb.edu/morph. A ruler was included in the pictures and its two endpoints were digitalized as the two last landmarks of the configuration.

Morphometric Methods **-** Geometric morphometrics was used to study the ontogeny of shape. Shape coordinates were used to construct the illustrations and the partial warps were the shape variables employed in the analysis. Landmark locations were transformed to shape coordinates by selecting two points (landmarks 11 and 20) to serve as the endpoints of a baseline as assigning them the coordinates (0,0) and (1,0). All specimens are then transformed to the same baseline orientation and length, a transformation that does not change the shape of landmark configurations (BOOKSTEIN, 1991). The coordinates that are not fixed are interpreted as the third vertex of a triangle drawn to the baseline. Partial warps are later calculated from the shape coordinates. The partial warps are geometrically orthogonal components of a deformation modeled by the thin-plate spline (BOOKSTEIN, op. cit). The deformation is decomposed into two components (the uniform and the no uniform) the measure of size was the centroid size.

The superposition are carried out using BigFix6 and CoordGen6f, which are part of the Integrated Morphometrics Programs (IMP series, by David H. Sheets; 2000) and that are freely available at http://www.canisius.edu/~sheets/morphsoft.html. BigFix takes bilaterally symmetric raw data from the digitizer program TPSDig, reflects the landmarks of the bilateral points, and produces files of Shape coordinates. The software CoordGen6f (IMP series) give the Procrustes superimposition.

Furthermore, we usedd pairwise resampling-based F-tests (N=100) to compare the mean shapes between males and females of each species and to measure the significance of differences between sexes in Partial Procrustes Distance units. This analysis is done in Two-Group6h (IMP). To examine when the sex became distinct, we ran the comparisons between each developmental stage. Using the Bonferroni method (SOKAL & ROHLF, 1995), an experiment-wise error rate of 0.05 was maintained by dividing the number of unplanned comparisons (three) to obtain the critical α value of 0.016.

Initially we compared male and female centroid size in each ontogenetic stage to determine if the sexes were dimorphic in size. The covariation between shape changes and size during ontogeny was compared between sexes too. Comparisons among their ontogenies were done by MANCOVA using tpsRegr (ROHLF, 1998; available at http://life.bio.sunysb.edu/morph). When slopes differ, three hypotheses were verified: (1) the sexes are distinct in the rate of development but they presented the same ontogenetic trajectory; (2) the sexes were distinct in their ontogenetic trajectories of shape but they are not distinct in their rate; or yet (3) the sexes are distinct in both rate and direction of ontogenetic transformations. This means that the sex could differ only by a scaling factor (e. g. the male shape could be simply a female shape “scaling-up”) -and that suggest that their slopes respond similarly to the same factor but at different rates- or they could repsond by different changes in slope, or in both. To distinguish among these possibilities the rate of change (rate of development) in shape for each sex and the ontogenetic trajectories of shape both were estimated and compared.

To know how the sexes differ when compared at a common size (using allometric scaling as a criterion of subtraction) we predicted the shape that would be observed at a given size in one sex and

compare the other with it, at that same size. We regressed shape on the natural logaritm of the centroid size and we used the regression equation to predict the shape of each sex at a given size. The mean of each sample is the expected shape of each sex at that size, and the variance within the sample comes from the residuals from the regression equation. This procedure was performed in Standard6 (IMP). That program removes the variation in shape correlated with variation in size (independent variable). From the coefficients of the regression of the shape data on the last column, the expected value for all the shape coordinates are calculated for a due value on the independent variable, then the residuals from the regression are added to that expected value (each residual is multivariate, meaning that each represents the deviation of an individual specimen from the expected value). We then test the hypothesis where the mean shapes are the same, using TwoGroup6h (IMP). TwoGroup6h also estimates the Procrustes distance between means and puts confidence intervals on that distance. We run this approach using the minimum and the maximum size for the male like reference and then repeat the same approach for females. So, we could observe the differences that remain after allometric scaling. Similarly, we standardized the shapes for each sex at the age 0 (zero) and 10 (ten) years (when all specimens are certainly mature). Here, the hypothesis that shape differences would be determined by size might be tested by predicting the shape that would be observed at a given size in one species, and comparing all the others to it at that same size.

Thus, we regresseded shape on standard length and used the regression equation to predict the shape of each species at the adult size of *O. byronia* (because it is the largest). In effect, we grew all three species to the largest of the three sizes. To attain this aim, we employ Standard6 to predict the shape of each natural logarithm. We then tested the hypothesis that the mean shapes are the same using a multivariate analysis of the variance and a Canonical Variates Analysis. These were performed in the software CVAgen6j (IMP).

After that, pairs of species were compared using TwoGroup, which both test the null hypothesis that the means do not differ and estimates the Procrustes distance between means (and puts confidence intervals on that distance). It is interesting to know by how much each differs and whether they differ from each other by more when compared at the same adult size than when compared at their actual adult sizes.

To determine the rates of development, the rate at which shape progressively differentiates away from that of the youngest age class was measured. That degree of differentiation was calculated by the morphometric distance between each individual and the average of the youngest age class in Procrustes Distances units (BOOKSTEIN, 1996). The rates were obtained by the multivariate regression of the Partial Warps on log-centroid size and the differences between rates of change related with an independent variable (centroid size) is tested by a Multivariate Analysis of Covariance. The ontogenetic changes in shape of males and females of each one of the three species was studied by multivariate regression of shape on size by Regress6K (IMP). Each full set of partial warp scores (plus the scores on the uniform component) was regressed on log-transformed centroid size (since that mostly of the ontogenetic shape change occurred is early in ontogeny). The significance of the percentual of the explained variance was tested by bootstrap (N=100). The number of the randomized set generated was determined by the stabilization criterion (MANLY, 1997). The results are the vectors of ontogenetic allometric coefficients. So, the components of these vectors are regression coefficients for the shape variables on the centroid size. The null hypothesis was that shape develops isometrically.

Statistical analyses were performed by comparing ontogenetic allometries of successive phases statistically. The vector that describe the ontogeny of shape over a given phase of development in each

species (e. g. juvenile to subadult, subadult to adult) was obtained by means of a piecewise multivariate linear regression of shape on size (like explained above) and normalized to the unit length. After that, the comparisons between the vectors from different ontogenetic stages were carried out by the estimation of the angle and the correlation (cosine) between the mentioned vectors. The angle is the inner product of vectors of allometric coefficients. So, it is possible to test the null hypothesis that the trajectory of shape is conserved during all the species ontogeny (when the angle between the vectors will be 0,0º, the cosine will be 1) using a resampling procedure to obtain confidence intervals for the angles and, the uncertainty around each trajectory (EFRON & TIBSHIRANI, 1993). This is very important because treating this angle of 0.0° as the null hypothesis is unrealistically narrow. The null hypothesis is that the angles between the ontogenetic phases are no larger than we would expect from the variation within a single phase but, is expected variation anyway. The question here is how much the uncertainty of the estimation of each trajectory (due to sampling) is so large that we can not reject the null hypothesis of no difference in ontogeny of shape. Initially, we tested if the observed angle could have been originate by two independent samples from the same ontogenetic phase by estimating the distribution of angles that could be obtained from repeated sampling of the ontogeny of a single group. The expected shape at each size is estimated from the multivariate regression equation, and residuals are calculated for each individual. Consequently, each specimen gives a multidimensional set of residuals representing its deviation from the expected shape for its size. The complete set of residuals for each individual is bootstrapped (N=100) with replacement as an entire set, thereby preserving the covariance structure among variables. After that, a replica of the original data set is produced by the addition of the set of residuals to the expected shape for each given size. Then, two ontogenetic vectors are derived from a pair of these randomic sets and the angle between them is calculated. When the observed angle between phases exceeds the 95% confidence interval of the two within-phase ranges, the difference between the vectors of the two stages is considered statistically significant. Otherwise, the differences in the sample sizes of the ontogenetic stages were taken in account in the distribution of the randomized data sets (the bootstrapped datasets took as references have comparable sample sizes). In this context, the two bootstrap sets formed from the group with the largest sample size agrees with the sample sizes of the two groups that were in comparison (what means that one bootstrap set has the larger sample size of the original group and the other has the smaller sample size of the other original group). In the other way, the two bootstrap sets formed from the data of the group with the smaller sample size both have that sample size because it is wrong to perform a bootstrap with a sample larger than the original data set. The comparison between vectors were performed in VecCompare6 (IMP).

We also tested another null hypothesis, which predicts that the similarity between species is no greater than expected by chance[28]. To perform this test, we randomly reshuffled the observed allometric coefficients 400 times, asking whether the angle between two observed vectors exceeds that found by comparing either to a vector of randomized coefficients. This procedure preserves the range of values found in the data, and also the proportion of isometric and allometric coefficients (positive and negative ones). When the observed correlation exceeds the 95% upper bound of correlations among randomized coeffficients, the null hypothesis of no greater similarity than expected by chance is rejected. That analysis is performed in Shuffle Allometry (IMP Series).

[28] Parts of ontogenetic vector that are significantly different could be more similar than expected by chance or no more similar than expected by chance even if they do not differ significantly (which usually are associated with small sample size)

The level of disparity between sexes is calculated in agreement with ZELDITCH et al (2003a) and FOOTE (1993). Confidence limits were placed on the Procrustes Distances by bootstrapping, considering the variability among individuals at the same size and the uncertainty of the regression. That is, the residuals estimated from the regression were drawn with replacement at random and added them to the expected shape, forming a bootstrap data set for each species. In the sequence, the same regression model was fitted to the bootstrapped sets and the size correction was carried out on the bootstrapped sets. The result is a bootstrap set for each species that incorporates the uncertainty of the regression. These calculations were done by DisparityBox6g, another freely available program in the IMP series.

To test the significance of differences in levels was of disparity between sexes, we used a bootstrapping procedure based on standardized data and considering the uncertainties of the regression. When placing confidence intervals on disparity, we removed individual specimens but not taking account the intraspecific variability. Considering that one of the difficulties found in calculating of the level of disparity is the differences in shape related with differences in size (allometry) and its influence in the disparity, the level of disparity was studied without and with correction for size. That means that we fitted a regression model to the data, determining the residuals and producing size-standardized data set. In this context, we measured the disparity with and without correction for size. In the last case, we measured disparity with correction to the mean size of each subsample and with correction using the same size for the two samples. In addition, the Partial Disparity that is the contribution to disparity of each subsample analyzed was calculated, again using Disparity Box6g.

RESULTS

Males and females do not differ in mean shape until late in ontogeny. This implies that the Means of the Partial Procrustes Distances between males and females (both, in the samples of juveniles and in the samples of subadults) were not significantly different with or without standardization for the same size (mean size of each age group considered) ($p>0.05$). This context is changed in the comparisons using the adults, where the means were different with and without standardization for the same size ($p=0.01$), in all species (Table 2; Fig. 2).

It is very obvious that the skull shape of fur seals was more narrow in general, but the differences in mean shape are different in each species.

Table 2. Partial Procrustes Distances (PPD) between the means of adult females and males. The first row of each species presents the values, the confidence intervals and the significance level for the distance for the specimens not standardized for size. The second row presents the results using data where the specimens were standardized for the same size. The mean size of the adults of each species was employed to standardize (both sexes).

	Partial Procrustes Distance between means	Confidence Intervals (95th percentile Range)	Significance Level
A. australis	0.0274	0.245 - 0.0367	p=0.01
	0.0378	0.0336 - 0.0464	p=0.01
C. ursinus	0.0407	0.344 - 0.0531	p=0.01
	0.0423	0.0374 -0.0522	p=0.01
O. byronia	0.0540	0.0396 – 0.0676	p=0.01
	0.0417	0.0351 – 0.0515	p=0.01

Similar results were found when the standardization was based in the maximum size of females and males in each species[29]. So, the differences between sexes can not be explained only by their differences in size and the species are not significantly different in the degree of dimorphism in ontogeny (Table 3). However, without standardization there is not superposition (in terms of PPD between sexes) between *A. australis* and *O. byronia*. On the other hand, in which concerns size (CS), only the juveniles[30] of *C. ursinus* presents the same means for both sexes (*A. australis* and *O. byronia* specimens have means significantly different between sexes in any stage of ontogeny; $p<0.01$)

Table 3. Partial Procrustes Distances between adult males and adult females standardized for the same size in each species. Confidence intervals at 95th percentile range are in parentheses (p=0.01).

	STANDARDIZED AT MAXIMUM SIZE OF FEMALES	STANDARDIZED AT MAXIMUM SIZE OF MALES
A. australis	0.0335	0.0443
	(0.289-0.0387)	(0.0401-0.0488)
C. ursinus	0.0376	0.0487
	(0.0340-0.0449)	(0.0446-0.0548)
O. byronia	0.0446	0.0600
	(0.0411-0.0511)	(0.0555-0.0662)

[29] Except when *O. byronia* specimens were standardized to the maximum male size.
[30] The centroid size mean is different between subadult females and subadult males of this species ($p<0.01$)

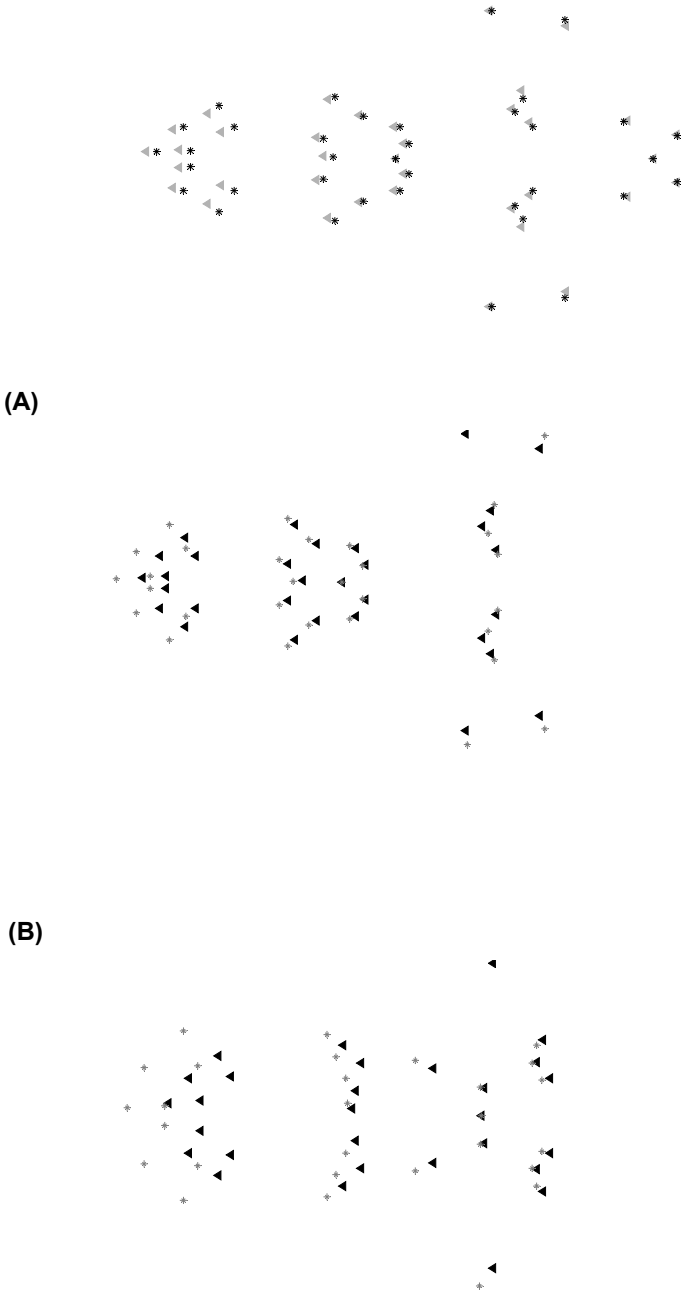

Figure 2. Comparisons of the mean shape between adult females (dark symbols) and adult males (grey triangles) of each species examined using Bookstein shape coordinates. (A) *Arctocephalus australis* (B) *Callorhinus ursinus* (C) *Otaria byronia.*

The general pattern of the dimensions along the species maximally differ it is similar when we analyze different ontogenetical or sexual groups (juveniles, subadults, adult females and adult males): two significant axes were detected, no specimen is misclassified by the discriminant function and the values of probabilities is small (always smaller that 10^{-6}).

But, in which concerns the axes that optimize group differences between the ontogenetic phases relative to within-group variation the species presents different patterns: in *A. australis*, there is only one significant axis of Canonical Variate (p=0.0019) when we compare sex and four specimens are misclassified (2 males and 2 females). When we considered in the analysis juveniles, subadults and adults again we observed only one significant axes ($p=6.5 \times 10^{-14}$), which separates clearly immature from mature animals. Here, 6 juveniles were misclassified as subadults and four subadults were misclassified as juveniles. When we form groups by age categories and sex in each species (3 significant CV axes, for 6 groups in comparisons), nearly only the juveniles are incorrectly classified (females are always classified correctly). In addition, the adults are separated from the imatures by the CV1 and themselves (males and females adults) are separated by the CV2 (Fig. 3).

Table 4. Groups from CVA-Distance Based in *Arctocephalus australis* specimens. Original Groups along rows and CVA groups along columns. Numbers in bold represent the number of misclassified specimens in each subgroup (JUV. = juveniles).

		MALES			FEMALES		
		JUV.	SUBADULTS	ADULTS	JUV.	SUBADULTS	ADULTS
MALES	**JUVENILES**	12	**3**	0	0	0	0
	SUBADULTS	0	9	0	**1**	0	0
	ADULTS	0	0	14	0	0	0
FEMALES	**JUVENILES**	0	0	0	14	**2**	0
	SUBADULTS	0	0	0	0	6	0
	ADULTS	0	0	0	0	0	15

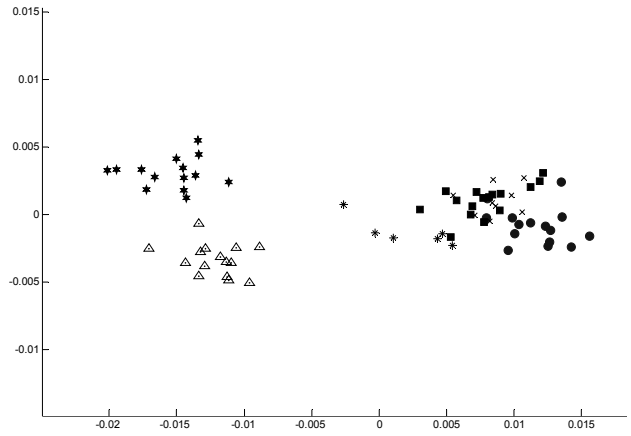

Figure 3. Scatter plot of the first two axis of Canonical Variates of groups that consider sex and group age in *Arctocephalus australis*. Circles=juvenile males, x=subadult males, stars= adult males, squares=juvenile females, asterisk= subadult females, triangles=adult females.

In *C. ursinus* only one axis is significant (p=0.0026) when we compare sexes and any specimen is incorrectly classified by the discriminant function. The function classified correctly all specimens too when the groups compared are the age groups but this time two axes are distinct (CV1 $p=1.75x10^{-7}$; CV2 p= 0.021). Juveniles are separated from the other two groups by the CV1 and CV2 distinguish subadults from the other two groups. The analysis considering the groups by age group + sex present not a misclassified rate either, and again three CV´s are significantly distinct (CV1=6.22 X 10^{-10}; CV2=0.0003; CV3=0.0335), but in the scatter plot of the 2 first Canonical Variates we can distinguish 3 groups that do not overlap each other (adult males, adult females and subadults and juveniles (the two last groups are distinguish basically by the CV2) (Fig. 4).

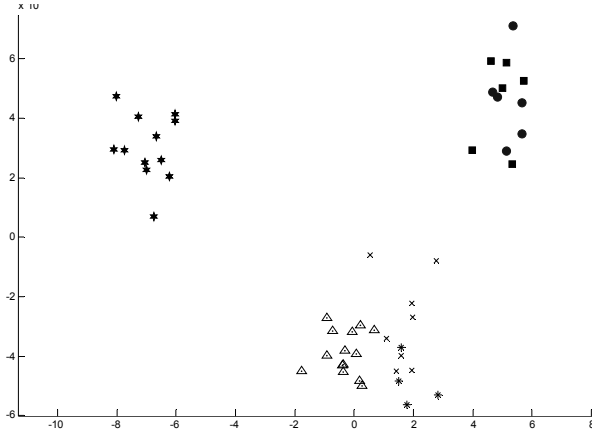

Figure 3. Scatter plot of the first two axes of Canonical Variates of groups that consider sex and group age in *Callorhinus ursinus*. Circles=juvenile males, x=subadult males, stars= adult males, squares=juvenile females, asterisk= subadult females, triangles=adult females.

In which concerns *O. byronia*, again one axis is significant in the comparisons between sexes (p=0.0001) but the misclassification rate is high (over all when all the ages are pooled together and the adult females and subadult males are many times confused): 9 males and 2 females were classified erroneously. The confusions between adults and subadults is verified another time in the analysis of the age class (2 significant axes; CV1 $p= 5.55 \times 10^{-16}$; CV2 p= 0.038) when three subadults and four adults are misclassified. But it is possible to visualize better the points of mistake when we observe the results of the Canonical Variates analysis using the age/sex groups (Table 5, Fig 5.) Juveniles are separated from the second group of points by the CV1 and CV2 distincts subadults from the adult males (Fig. 5). Subadult and adult females are highly confounded, subadult males are occasionally confounded with adult males, but the juveniles are misclassified in any sex (Table 5).

Table 5. Groupings from CVA-Distance Based in *Otaria byronia* specimens. Original Groups along rows and CVA groups along columns. Numbers in bold represent the number of misclassified specimens in each subgroup (JUV. = juveniles).

		MALES			FEMALES		
		JUV.	**SUBADULTS**	**ADULTS**	**JUV.**	**SUBADULTS**	**ADULTS**
MALES	**JUVENILES**	7	0	0	0	0	0
	SUBADULTS	0	13	**1**	0	**3**	**2**
	ADULTS	0	**2**	19	0	0	0
FEMALES	**JUVENILES**	0	0	0	5	0	0
	SUBADULTS	0	**2**	0	0	9	**6**
	ADULTS	0	1	0	0	4	10

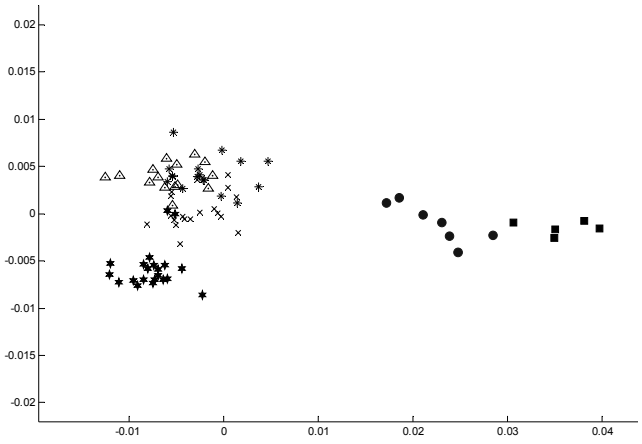

Figure 5. Scatter plot of the first two axes of Canonical Variates of groups that consider sex and group age in *Otaria byronia*. Circles=juvenile males, x=subadult males, stars= adult males, squares=juvenile females, asterisk= subadult females, triangles=adult females.

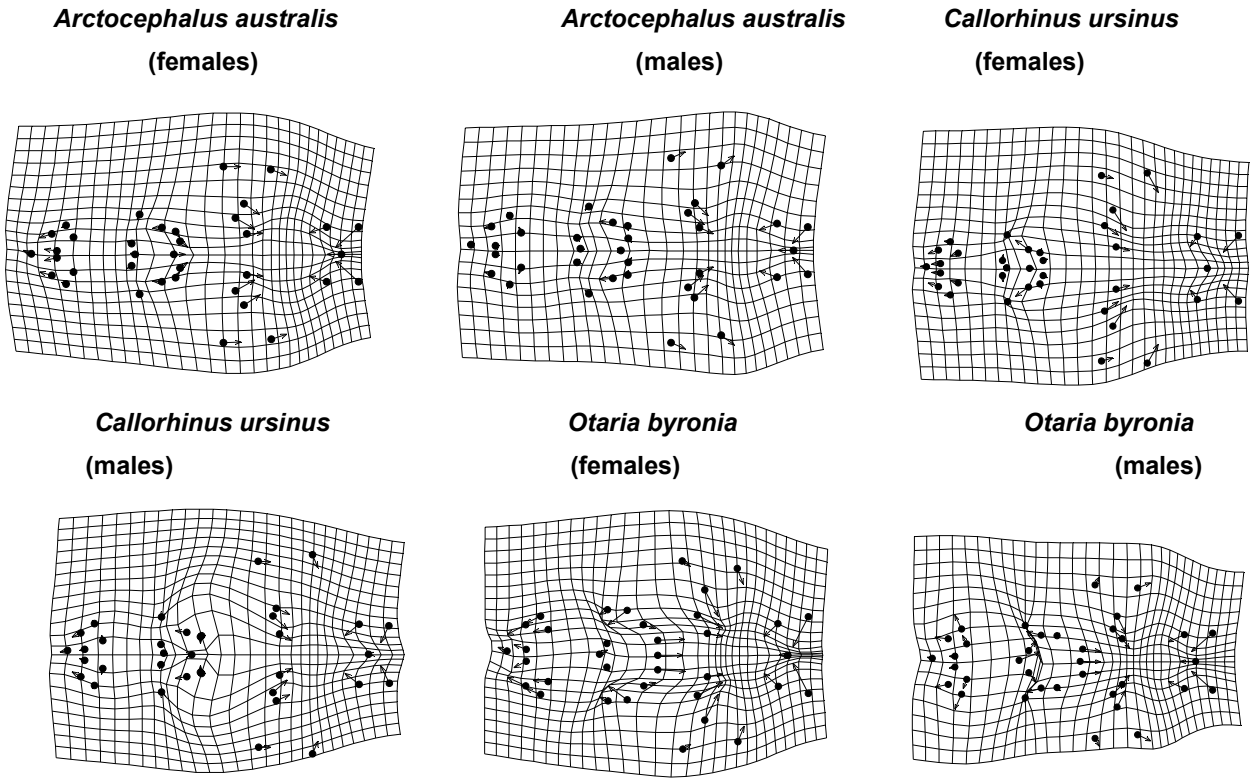

Figure 6. Ontogenetic transformations in shape for each species/sex subsample (dominant linear trend) using the whole configuration of landmarks. These transformations were depicted as the deformations implied by the first principal component using the "thin-plate spline" method .

We can notice in the ontogeny of the females of *A. australis* an elongation of the rostrum, alveolar series and of the coanas. The landmark that is in the zigomatic arch and that one that is in the mastoid process are displaced and all the braincase became shorter and more straight to the other regions of the skull (which can be detected in all the sub samples analyzed). In the rostrum of the males, the changes seem to be less conspicuous (what we can observe clearly in the absence of important changes in the landmarks above the incisive foramen or in the coana). The braincase follow the same pattern shown by the females, as mentioned above, but the zigomatic arch and the mastoid process are displaced more distally and posteriorly.

The females of *C. ursinus* present a small enlargement and deepening of the most posterior extremity of the alveolar process, the landmark that is in the zygomatic arch is a few displaced posteriorly and the mastoid process tighten a lot. But in the males, the more strike changes in ontogeny resides in the rostrum that became narrower and more specially in the region of the coana, a region where it is possible to detect a lot of developmental changes and amplification in that group). The zigomatic arch and the mastoid process displaced posteriorly, but the mastoid process moves medially too.

Finally, in *O. byronia* (both sexes) the palate became longer (the coane is displaced posteriorly). The antero-posterior growth of the palate of *O. byronia* is very characteristic of this species specifically. The rostrum of the females became narroweer while that of the males became wider. A similar pattern can be seen in the zigomatic arch. The mastoid process of the females displaces in direction to the midline during

ontogeny, but that of the males is displaced laterally.

The null hypothesis of isometric growth is rejected ($p < 0.001$) for all species/sex subsamples analysed (Table 5).

Table 5. Rates of divergence away from the initial shape, estimated by the regression of the Procrustes distance between each specimen and the average of juvenile form of its species on log-transformed centroid-size.).

		RATE	SE	R^2
A. australis	**FEMALES**	0.1130	0.0139	0.8081
	MALES	0.1039	0.0104	0.8537
C. ursinus	**FEMALES**	0.0657	0.0164	0.6314
	MALES	0.0653	0.0089	0.6431
O. byronia	**FEMALES**	0.0442	0.0089	0.6431
	MALES	0.1341	0.0108	0.8801

The slopes of each sex in *A. australis* and *O. byronia* are heterogenous ($p<0.01$ and $p< 0.0034$, respectively). Males and females only share a common rate of ontogenetic transformation in *C. ursinus* ($p= 0.0515$). However, males and females of *C. ursinus* are significantly different in proportions at the outset of growth (intercepts are different and that distinction persists throughout all of growth). But the changes in direction on the ontogenetic trajectories can be documented more rigorously if we test the allometric patterns (Table 6). Sexes of *A. australis* and *O. byronia* are significantly different from each other (the correlation is significantly different from one) but in the case of *C. ursinus* they are more similar than expected by chance (the correlation is higher than zero, but not significantly). However, the observed correlation exceeds the 95% upper bound of correlations among randomized coefficients, we reject the null hypothesis of no greater similarity than expected by chance.

Finally, the disparity is similar to the pattern revealed in the CVA analysis: in *A. australis* increase gradually and the disparity between the two sexes of adults is small, especially when we corrected for size. The disparity between the juveniles and the subadults is nearly four times higher in *C. ursinus* that in *A. australis*, but the level of disparity between the different ontogenetic stages is more or less constant (so, the disparity between the adults is nearly four times higher in *C. ursinus* that it is in *A. australis*). In the sea lion *O. byronia* the higher level of disparity is relatively early in ontogeny, between the juveniles and the subadults. The subadults versus adult females present the smaller disparity in morphology. We can in addition detach that the disparity between the juveniles and the other ontogenetic stages are extremely striking, increasing gradually (Table 7). The standdarization do not do a striking difference due to the small difference in size between the stages compared in the same species.

Table 6. Comparisons between ontogenetic trajectories of males and females in each studied species. Angles statistically different from 0.0º are in bold (p<0.05).

	BETWEEN MALES AND FEMALES	VECTOR CORRELATION	WITHIN FEMALES	WITHIN MALES
A. australis	**29.8**	0.86776545	25.6	22.4
C. ursinus	37	0.79863553	30	39.4
O. byronia	**37.8**	0.79015501	20.8	20.2

Table 7. Level of disparity between ontogenetic and/or sex groups of *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*. The values in the first line of each case is the level of disparity understandarized and the values in the second line is the correspondent level with the samples standardized in respect to size. The numbers in parentheses are the confidence intervals.

	A. australis	***C. ursinus***	***O. byronia***
juveniles x subadults	0.00023 (0.00027-0.00077) 0.0017 (0.0009-0.0034)	0.00117 (0.00069-0.00264) 0.0028 (0.0012-0.0064)	0.00415 (0.00320-0.00077) 0.0111 (0.0087-0.0218)
juveniles x adult females	0.00212 (0.00178-0.00280) 0.0051 (0.0038-0.0076)	0.00163 (0.00116-0.00289) 0.0035 (0.0026-0.0055)	0.00592 (0.00520-0.00830) 0.0145 (0.0123-0.0261)
juveniles x adult males	0.00227(0.00186-0.003) 0.0071 (0.0058-0.0104)	0.00316 (0.00239-0.00450) 0.0063 (0.0050-0.0084)	0.00934 (0.00740-0.01289) 0.0197 (0.0165-0.0300)
subadults x adult females	0.00116 (0.00091-0.00197) 0.0016 (0.0013-0.0025)	0.00116 (0.00091-0.00197) 0.0016 (0.0013-0.0025)	0.00033 (0.00029-0.00076) 0.0008 (0.0006-0.0016)
subadults x adult males	0.00139 (0.00112-0.00208) 0.0034 (0.0023-0.0048)	0.00128 (0.00101-0.00243) 0.0018 (0.0010-0.0041)	0.00172 (0.00128-0.00274) 0.0030 (0.0024-0.0042)
adult females x adult males	0.00037 (0.00038-0.00081) 0.0013 (0.001-0.0027)	0.00128 (0.00105-0.00151) 0.0019 (0.0012-0.0034)	0.00146 (0.00108-0.00253) 0.0025 (0.0019-0.0040)
females x Males	0.00011 (0.00015-0.00045)	0.00035 (0.00025-0.001)	0.0005 (0.00041-0.00133)

Table 8. Level of disparity (Distance-based disparity based on the group means working with all loaded groups-bootstrapped size correction between males females) between males and females of *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*. The numbers in parentheses are the confidence intervals.

	A. australis	***C. ursinus***	***O. byronia***
STANDANDIZED FOR THE MINIMUM SIZE	0.0172 (0.0105-0.0376)	0.0214 (0.0171-0.0542)	0.0753 (0.0539-0.1212)
STANDARDIZED FOR THE MAXIMUM SIZE OF THE FEMALES	0.0129 (0.0098-0.0282)	0.0165 (0.0110-0.0389)	0.0246 (0.0154-0.0381)
STANDARDIZED FOR THE MAXIMUM SIZE OF THE MALES	0.0119 (0.0082-0.0239)	0.0154 (0.0122-0.0406)	0.0224 (0.0153-0.0376)
STANDARDIZED FOR THE RANGE OF SIZE OF THE FEMALES	**0.0058 (0.0045-0.0076)**	**0.0061 (0.0036-0.0088)**	**0.0150 (0.0123-0.0194)**
STANDARDIZED FOR THE RANGE OF SIZE OF THE MALES	**0.0046 (0.0037-0.0060)**	**0.0079 (0.0051-0.0115)**	**0.0098 (0.0083-0.0123)**

DISCUSSION

The degree of dimorphism in adults is not significantly different between species. In which concerns the dimorphism in adults, the difference observed in the results of the shape comparisons between the sexes in *O. byronia* is due to the extreme size of the males of this species. The differences in shape between sexes found only in adults agrees with the argument that the sexual dimorphism in taxa with larges males have commonly revealed an interspecific pattern of allometric extrapolation where as size increases, also the degree of sexual size dimorphism increases, (ADAMS & FUNK, 1997) which suggest a role for sexual selection on male size, an old issue in the literature of the otarid where the adult males are polyginic (BRUNNER, 2000).

There is a lot of evidences in mammals that suggests a relationship between social structure and sexual dimorphism, but it can be explained as a result of male intrasexual selection or asa result of ecological specialization of different sexes to different food resources (or yet it could be a combination of these and other factors). Species in which males are significantly larger then females almost always have polygynous breeding systems, and the degree of dimorphism is correlated to some extend with size of the breeding group (ALEXANDER et al., 1979), although there arebody size, ecology, and substrate differences.

Large size has been shown to be correlated to large dimorphism across many animal taxa to the degree that it has been regarded as one of the rules of ecology: Rensch's rule size dimorphism might be the consequence of many different selection pressures, and to study the effect of one particular cause, one needs to isolate it from the others (LINDENFORS & TULLBERG, 1998). On the other hand, some analyses in pinnipeds also revealed a significant relationship between harem size and body size. These results support the hypothesis that sexual size dimorphism in that group is the product of an exclusive male response to sexual selection. Most importantly, however, is that it was demonstrated a relationship between the degree of sexual selection on males and male body size per se (LINDERFORDS, 2002). The argument most commonly cited is that large body size in males of many species may have evolved because of the advantages of large size in promoting success in male-male combat, hence presumably increasing opportunities for mating. Similar hypotheses have been advanced concerning the effects of female choice, mate sequestration, and several other factors or niche divergence between the sexes (an ecological cause for the evolution of sexual dimorphism).

Another line of evidence for the role of sexual selection comes from the ontogenetic timing of onset of the dimorphism. This is not to deny, however, the overwhelming importance of the general concept of heterochrony in determining sexually dimorphic morphology; it seems often to be true that males and females follow similar developmental paths, but that one sex progresses much further than the other. This must be investigated appropriately testing the hypotheses of heterochony. The second category of sexual dimorphism resulting from niche divergence encompasses species in which different sexes feed on different things, and differ in trophic morphology in ways that seem to reflect these dietary differences. In fact, females and males of *O. byronia* feed in different niches (CRESPO, personal communication). But obviously, sexual differences in diet are almost inevitable if the sexes differ greatly in body size. Body size may also influence habitat use and diet through secondary effects on predation vulnerability or social dominance.

In most vertebrates, the sexes are nearly identical in morphology during early development and undergo highly divergent growth to achieve different adult sizes and recent studies show that the rapid evolution of sex-specific developmental regulators and modifiers can produce sexual dimorphism in size

whilst maintaining the integrity of the developmental program that is shared between sexes (BADYAEV, 2002). Sexually dimorphic size traits that are expressed only in late ontogenetic stages (and therefore do not require extensive developmental integration with other traits) should develop with the lowest intersexual conflict. Species with longer growth periods experience more age-specific selection pressures and thus are more likely to evolve greater dissociation in growth patterns between the sexes. Tipically, SSD is favored by selection acting during adult stages when differences in size contribute to the reproductive success of both sexes. Furthermore, because of their roles in reproduction, males and females are often under selection that favors their divergent morphological appearance. Yet, sexes share most of the genes that control basic aspects of growth, and sex-biased expression of these shared genes during development is required to accomplish adult sexual size dimorphism (FAIRBAIRN, 1997). At each development stage, discordance between the realized expression of genes in both sexes and the degree of sex-biased expression of genes that is favored by selection on each sex sets the stage for intersexual ontogenetic conflict, which is more pronounced in complex traits, such as body size, that requires prolonged and coordinated development, and where the evolution of sex-specific expression is likely to be slow (RICE et al, 2001).

From the CVA analysis, it is interesting to notice that juveniles of the sea lion are more distinct in shape than any other ontogenetic stage (besides the fact of the sexual dimorphism being stronger in the adults), which is not an issue in the fur seals. In the later, the adults are generally more apart from the other ones. It is also interesting too to note the perfect classification performed with the *C. ursinus* specimens.

The canonical variates are a convenient reference system used to most efficiently description the greatest differences among the populations under study. But we should consider that the computation of the canonical variates involves rescaling[31], and the interpretation of the scores can be complex[32]. It is important to maintain in mind that the direction in which group means are most different is not necessarily the direction in which individuals are most different. In fact, biological and statistical variation is not always concordant and that information of biological importance may be obliquely related to the major axes of statistical variation (ZELDITCH et al, in press). But, anyway, the scores and the axes provided are a tool to analyze morphology in search for answers to biological questions. What is important is to take in account is the full canonical variate space. That way, CVA will always be an approach that maintains the classical purpose of analyzing variation and covariation of the comparative anatomy within and among populations with the aim o explain the diversity and the meaning of the biological shape.

A. australis is the second more accelerated in the ontogeny (after *O. byronia* males), with the higher rate. We observed a striking differences in the rate of divergence away the initial shape between the males and females of *O. byronia*. The males are apporximmatly like 3 times faster than the females, which could suggest a heterochonic pattern actuating in the evolution of the dimorphism. However, the species (not only *O. byronia*) also differ in their ontogenetic transformations (allometric pattern) rather than progressing along the same ontogenetic trajectories at different rates. Besides that males and females of *A. australis* are different in the allometric coefficient, the magnitude of the difference in not so large. The sexes of *O. byronia* are different again inn respect to the determination coefficient (r^2), where the males present the higher correlation between the procrustes distances and the log-transformed centroid size. The differences between sexes of *C. ursinus* are apparently due to the interception of the regression, but in our samples it was not possible to detect dimorphism when comparing the juvenile samples. So, we can infer a heterochronic

[31] Optimization also involves rescaling such that the new axes are scaled differently from the original axes and scaled differently from each other.
[32] Distances on canonical variates are not equivalent to distances in the original space.

process in the origin of sexual dimorphism in this species, where males are peramorphic in relation to females, because they probably are post-displaced in comparison with the latter. However, the relationship between changes in shape and chronological age should be known to infer that cause relationship. The level of disparity between ontogenetical different stages is in agreement with the pattern showed in the canonical variate analysis.

Of course, since we are analyzing allometry using geometric data it is important to remember that the allometric coefficients no longer are meaningful in terms of a growth model, either the power law or a sigmoidal curve relative to time. They reflect shape changes with size. However, the different meanings of the coefficients do not impede our ability to recognize the evolutionary patterns of the evolving ontogenies if we access the length of the trajectory of each sex/species group. In fact, it is known that the two developmental processes that generate sexual size dimorphism are sex-specific differences in growth rate and growth duration. These processes are the subjects of selection and their relative contribution to the sexual dimorphism of adults is informative about the direction and patterns of sexual dimorphism evolution.

Furthermore, the sexual dimorphism at birth and during early growth is strongly limited by the mother´s body size and by the costs of lactation and provisioning, which was shown for many pinnipeds species. (WILKINSON et al., 2001). Similarly, offspring sexual size dimorphism (SSD) during the lactation is low, because many times mothers do not provide males and females preferentially even in the most size-dimorphic species. For example, in *Mirounga leonina* and in *Arctocephalus gazella*, the maternal expenditure during lactation is equal between the sexes, but males are able to grow larger due to their lower metabolic rate compared with smaller, but more active daughters (ONO, 1996; GUINET et al, 1999). The lack of the sex-biased provisioning is a powerful selection pressure on the ontogeny of the larger sex, leading to the evolution of an increased rate and duration of growth as well as adaptations that allows greater sensitivity to environmental variation during growth.

Studies generally seem to indicate that male pups are heavier at birth and grow slightly faster, but that they do not receive more milk than female pups. For instance, ARNOULD et al. (1996) showed that although male and female Antarctic fur seal (*Arctocephalus gazella*) pups received equal amounts of milk, males directed more of this to lean tissue growth while females accumulated greater adipose stores. Since fat and lean tissue differ in terms of density and energy content, a lighter but fatter pup may still have received the same amount of energy and material from its mother as a bigger, heavier pup. In California sea lions (*Zalophus californianus*), however, dimorphism is reported to result from differential maternal expenditure in the two sexes (ONO & BONESS 1996). In general, the evidence for differential expenditure in the sexes seems rather tenuous (Trillmich 1996).

Change in dimorphism is a product of sex differences in changes of size and in order to study the evolution of sexual size dimorphism. One, therefore, first has to take into account the evolution of size itself (LINDENFORS & TULLBERG, 1998). But on the other hand, it is evident; size dimorphism is not a simple allometric function of size because a lot of trade-offs related to life-history and energy are in question (LINDENFORS & TULLBERG, 1998).

Even for species in which the evidence for differential expenditure is convincing, the fitness returns in terms of future survival and reproduction have not been measured. We can only conclude that factors related to sexual selection on males are of little importance in determining pinniped female size. Explanations for female size changes thus, have, to be investigated in another context. Selection for female size is likely driven by a complex set of trade-offs between factors such as lactation patterns, prey availability and a

balance between immediate costs of lactation (in terms of energy depletion) and future reproductive performance of females as well as offspring (e.g. COSTA 1991; POMEROY & FEDAK, 1999).

APENDIX 1. ANATOMICAL DESCRIPTION OF THE LANDMARKS

1- anteriormost point of the pré-maxilla tuberosity
2- antero-lateral extremity of third incisive alveolus
3- anteriormost point of incisive foramen
4- lateral extremity of canine alveolus
5- anteromedial point of first post-canine alveolus
6- anteriormost point of the maxilla-palatine suture
7- point that label the direction change of the maxilla-palatine suture
8- posteriormost point of the root at the lateral limit at bone palate of zigomatic process of the maxilla
9- posteriormost point of sixth post-canine alveolus
10- posteriormost point of palatine extension of maxilla (“pterygoid” process of the maxilla)
11- posteriormost point of interpalatine suture
12- point that label the direction change of the posterior border of palatine
13- posteriormost extremity of oval foramen
14- lateral extremity of jugal-esquamosal suture
15- medial extremity of the contact between the glenoid fossa and the ectotympanic
16- anteriormost extremity of the anterior aperture of carotid canal
17- antero-lateral corner of mastoid process
18- posteriormost point of the condiloid foramen
19- posteriormost point of occipital condyle
20- anteriormost point of foramen magnum.

CAPÍTULO IV

ONTOGENY AND PHYLOGENY: A CASE STUDY USING OTARID SKULLS (PINNIPEDIA: MAMMALIA)

ONTOGENY AND PHYLOGENY: A CASE STUDY USING OTARID SKULLS (PINNIPEDIA: MAMMALIA)

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ABSTRACT

The search for mechanisms that can generate major morphological changes has led to the study of ontogeny, in part because some kinds of modifications of ontogenies are a plausible way to generate major phenotypic change. Here, we examine the ontogeny of shape of *Arctocephalus ausralis*, *Callorhinus ursinus* and *Otaria byronia* using geometric morphometrics methods. Our central purpose is to study the relations between development and phylogenetical history using these species to represent the Otarid family. Thus, we describe the patterns found in comparative studies of these ontogenies, including developmental allometry. Ordination methods and the comparisons between the allometric vector of different ontogenetic phases reveal that the ontogenies can not be summarized by a single linear vector in any analyzed group, where *C. ursinus* ontogeny is the more linear and *O. byronia* have the more multi-dimensional species among the 3 that we had examined. Shape changes in the otarids studied here are more related with size that with age and anyone of the species shares a common growth allometry or a common ontogenetic trajectory/pattern. In the same way, shapes at onset or offset are not the same in any case. Whether ontogenetic trajectories are linear or curve could be a function of developmental timing or more specifically it could depend on the age at which allometries stabilize in post-natal ontogenies. The amount of differences in the ontogenies between species is in agreement with the phylogenetic relationships. Finally, we conclude that the changes in otarids skull ontogenies has occurred in spatial and temporal terms.

INTRODUCTION

The search for mechanisms that can generate major morphological changes has led to the study of ontogeny, in part because some kinds of modifications of ontogenies seem an elegant and economical way to generate major phenotypic change (GOULD, 1977). Now the search is on for examples of changes in ontogenies that have indeed been responsible for such novelty. In a fundamental way such changes must be part of the mechanism for much of the morphological diversity, since it is ontogeny that actually generates most of the phenotype. But incidences of particular ontogenetic phenomena and their importance to larger scale diversity remain poorly understood, in spite of a growing literature on the subject. One of the reasons for this lack of knowledge is that few researchers have used methods which can unambiguosly indicate which mechanisms of ontogenetic modification are involved. Perhaps the best known mechanism of ontogenetic change proposed as a source for evolutionary novelty is heterochrony. In evolution and development, there are two subjects that were focus by many studies: allometry and heterochrony[33]

In the history of Heterochrony it is possible to highlight two special moments: the books by GAVIN DE BEER *Embriology and Evolution* (1930) and *Embryos and Ancestors* (1940) and the publications by GOULD (1977) and ALBERCH et al. (1979). The latter acted, undoubtedly as the catalysis of a number of works on the heterochronic processes (e. g. RADINSKI, 1984) that have not yet supplied explicit descriptions of procedures for the detection and isolation of these results in nature (FINK, 1982) and the precise time measurement.

S. H. Rice (1997) emphasizes that there are more than six ways of modifying form and size during the ontogenies and during the phylogenies). Hence, considering the classic definitions of the results and

[33] The later implies the concept of time, which is not present in allometric studies.

heterochronic processes literally is to simplify the trajectories, which could transform the definition of heterochrony a synonym of morphologic evolution.

Following this conjecture is the polemic resultant from the interaction among the heterochronic premises related to dissociation and the growing discoveries/new methodological focuses for the evaluation of morphologic and form intergration. The past one and a half decades have witnessed a tremendous explosion in research on heterochrony – the evolution of ontogeny, but that considerable miscommunication characterizes the literature on heterochrony centered largely in the disparate ways in which heterchronic terms have been mathematically operationalized.

To detect heterotopy we need information on changes in spatial as well as temporal features of growth, so we need to identify changes in direction[34] as well as changes in rates and timings of ontogeny (ZELDITCH & FINK, 1996). The term was first defined by HAECKEL (1866) to describe cases in which an ontogenetic sequence of events did not recapitulate the phylogenetic sequence.

A prerequisite for an analysis of heterochrony is a phylogenetic hypothesis of the relevant taxa. With this in hand, the first step in recongnizing heterochronic change is to identify character transformations in the context of the phylogeny. The second step is to examine the ontogenies of the features. A third step is to categorize the change. Finally, depending on the research program underway, one might wish to determine whether this novelty is associated with other phenomena, such as marked changes in speciation rates (FINK, 1988).

But it makes sense considering that, any changes to rate of development, or to onset or cessation of growth can have profound effects on the descendant morphologies, particularly if growth is allometric McNAMARA (1996).

Analyses of heterochrony have typically relied on the Alberch et al. (1979) formalism, which classifies evolutionary changes into changes in (1) age at onset of development, (2) developmental rate, and (3) age at offset of development. Therefore, heterochrony is viewed as the most common type of evolutionary change in development. Alternative hypotheses such as heterotopy are little explored, although it could explain why morphologies differ more than expected under a hypothesis of heterochrony. Under a hypothesis of heterotopy, taxa do not only progress more or less rapidly along the same ontogenetic trajectory; they diverge in the spatial pattern of growth. If heterotopy and heterochrony both occur, taxa will progress more or less rapidly along divergent ontogenetic trajectories. Such a combination of processes, may be difficult to detect empirically when morphology is described in simple univariate charactersbecause one-dimensional characteristcs would always appear to be more or less developed in one taxon; (because there is no other way in which they could possibly differ). Being one-dimensional, these features necessarily both develop and evolve along the same dimension so they always suggest parallelism between ontogeny and phylogeny. But complex morphologies are not one-dimensional and can reveal more kinds of developmental patterns. Such changes in spatial pattern are rarely done in comparative studies of allometry that concentrate on the magnitudes of rates or intercepts. But ontogenetic allometry has positions on the organism, not just rates and spatial patterning can be just as labile as timings and rates. So, other possibilities are allowed by the geometry of the data.

[34] We are considering relative rates of change at each spatial scale, and to draw ontogenetic trajectories in morphospace, so now, by direction of ontogenetic change we mean the path through morphospace.

It is well known that the quantification of biological phenomena by means of mathematical models and statistical methods is an established practice, and more recently, we have seen a real revolution in the morphometric methods and concepts to describe the shape variation without lost of geometric information.

So, to examine the ontogeny of shape, we will emphasize geometric morphometric. These have two distinct advantages over more conventional methods for the analysis of heterochrony and heterotopy. First, the original models for heterochrony were framed in explicitly geometric terms. Inferences based on these models, if applied out of the context of the original dimensions, can be misleading. Second, geometric methods can analyze spatial relationships among landmarks, which are obviously useful for studies of ontogenetic spatial patterning, particularly in the highly complex mammal skull (where the shape variables correlated with size can change from age to age). Rather, development is epigenetic and diverse aspects of morphology are integrated during ontogeny. The vertebrate skull is typically viewed as a composite of multiple developmental and functional units, but these units need not be independent in either their development or their evolution (ZELDITCH et al., in press).

The three aims of this paper are: (1) to compare the ontogenies of three species of Otariidae: *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia* ; (2) to analyse the evolutionary patterns that had act in these otarids species ontogenies using geometric morphometric analyses (3) to understand the relations between development and phylogenetic history. We intend to describe the patterns that can be found in comparative studies of ontogeny, including developmental allometry. The latter is specially relevant considering its implications for form-function relationships and the highlights that it offers into morphogenesis, and growth and their spatiotemporal dynamics[35]. In effect, when we know the allometric coefficients we can better understand the spatial distribution of relative growth rates.

MATERIAL AND METHODS

Our samples comprise a cross-sectional ontogenetic series of skull of three otarid species: *A. australis* (n=76), *C. ursinus* (n=51) and *O. byronia* (n=84). For practical reasons, the first two species are refered here like “the furs seals”and O. byronia is named sometimes simply like “the sea lion”.

We use the number of growth layer groups deposited in the dentine of the bisected canine as our estimate of chronologicall age (SCHIAVINI, 1992) and the sutural ages to determine the ontogenetic stages (juveniles, subadults and adults) (SIVERTSEN, 1954). The analyses were performed considering species, sex, and sutural age groups (juveniles, subadults and adults).

Morphological parameters such as size are often used like a proxy for age, but this does not provide the information needed to determine which parameter (developmental rate or size) has been decoupled from the ancestral relationship to time. To detect it, we need age information.

In our analyses, we will use partial warps like variables. The landmarks (Fig. 1) were determined using the program TpsDig (with the endpoints of a ruler included) in the way that they may be recognizable in all plans previously photographed, for all species and taking in account the shape in the more appropriated way.

If landmarks do not explicitly archive information about the curving of form in-between them, in practice they seem to include enough of that information to fairly represent the statistics of the curving.

35 Evolutionary changes in the spatiotemporal dynamics of growth can be discovered by comparative studies of allometry.

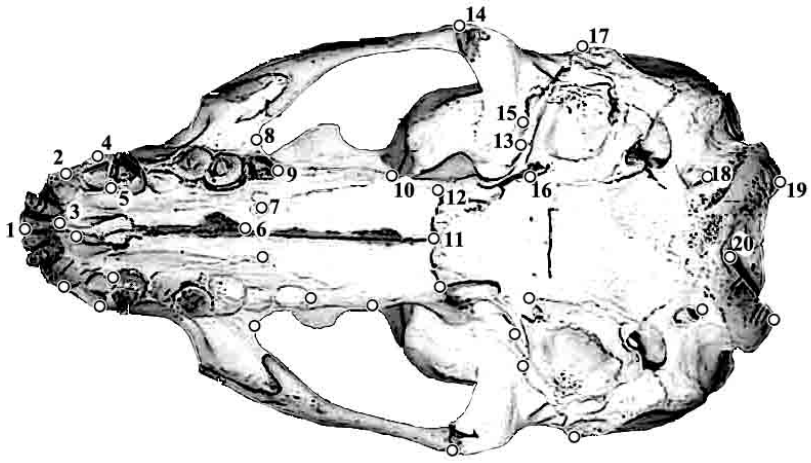


Figure 1. Landmarks shown on the skull of a juvenile of *O. byronia*. Descriptions of each landmark are given in Appendix 1.

Then, we constructed the shape coordinates for each landmark and we determined the mean shape for each age-group. The measure of size is in the last column. Therefore, we will described the ontogeny of the skull shape for each species in each plane photographed using Procrustes superimposition. This methodology made possible the comparison of the ontogeny of the shape in that plane. The following step for this study of ontogeny was to look at the changes in shape with increasing age/size of each species. It was analyzed by multivariate regression of shape on size. Each full set of shape variables (the full set of partial warp scores) were regressed on log-centroid size. The null hypothesis was that shape develops isometrically. After that, it will be applied the Thin-plates splines approach (to model the shape changes like landmarks deformations) and the statistical analysis.

But before runing a statistical test at face-value, it is important to check the assumption of linearity by determining the Procrustes Distance between each specimen and the average of individuals with the lowest values on the independent variable. If the assumption met, we expect a linear increase in that distance with increasing values of the independent variables. The assumption of linearity enters into the analysis in a more subtle way, but equally important. We are also assuming that the shape variables correlated with size do not change from age to age-that shape changes in the same direction over the whole course of ontogeny. However, this assumption will fail if the direction of shape modifies according to the independent variable. In these cases, we are not able to represent the ontogeny of shape by a single vector of coefficients because that vector changes direction with time. The ontogenetic trajectory in such cases will be a curving path in shape space, not a straight line.

To determine whether ontogeny of shape can be characterized by a single linear vector, we used a combination of ordination and statistical methods. Ordinations were carried out using principal component analysis (PCA) to determine whether age-related variation lies along a single component, or instead, requires multiple dimensions, perhaps even exhibiting reversals along one or more axes. Statistical analyses are performed by comparing ontogenetic allometries of successive phases statistically, which document more rigourosly the changing directions of the ontogenetic trajectories can be documented more rigourously by comparing phases. The vector of allometric coefficients describing the morphogenesis of each sex was estimated by multivariate regression of shape on size, as described above. Another time, to compare these

vectors multivariately, the angle between them were calculated and the range of the angles within each sex that agrees with the original data sets were estimated. Thus, to estimate the uncertainty of the trajectory due to sampling, the residuals were calculated from the regression of shape on size such that each individual gives a multidimensional set of residuals describing its deviation.

The analysis of covariance is the conventional approach to test the hypothesis of allometric scaling (when species do not differ in shape when compared at a common value of the covariate). But when the data are multivariate, the context is more complex (the allometric scaling is not the only possibility). Species could be, for example, distinct because they differ in the initial shape but they follow identical ontogenies after that, attained different sizes. In bivariate analyses, this is known as "transpositional allometry"[36]. Additionally, species could differ because they follow different ontogenies of shape but they attain the same adult body size (and they could differ in combinations of juvenile shape, ontogeny of shape and adult size too).

So, when we know how the species differ when compared at a common size, we are using the allometric scaling as a criterion of exclusion. So, the hypothesis is tested by predicting the shape that would be observed at a given size in one species, and comparing all the others to it (at that same size). Usualy, the basic hypothesis tested in studies of heterochrony is if the allometric scaling in ontogeny of one species can predicts the shape of another at a given size. We might want to know if different species follow a common ontogenetic trajectory at different rates (i.e., if they evolve by heterochrony). These kinds of analyses involve more than just estimating the relationship between size and shape in a population, they require testing the hypothesis that the populations do not differ in other two parameters: (1) the rate of response of shape to the independent variable: (2) the direction of the response (the direction of the vector of effects).

We regressed shape on Natural logaritm and used the regression equation to predict the shape of each species at the adult of *Otaria byronia* (because it is the largest). In this manner, we were growing all three species to the largest of the three sizes. To predict the shape of each natural logarithm we employed the Standard. The mean of each sample is the expected shape of each species at that size, and the variance within the sample comes from the residuals from the regression equation. After that, we tested the hypothesis that the mean shapes were the same using a multivariate analysis of the variance and a Canonical Variance Analysis. These were performed in the software CVAgen6j (IMP series, SHEETS, 2000).

Then, pairs of species were compared using Two Group, which both test the null hypothesis that the means do not differ (and we also estimate the Procrustes distance between means and puts confidence intervals on that distance). This is very interesting because we can know by how much each differ and whether they differ from each other by more when compared at the same adult size than when compared at their actual adult sizes. Finally, we tested if the species were more or less different than that if compared at *Callorhinus ursinus* smaller adult size (so the difference between them is not simply an effect of extrapolating both to the relatively large size of *Otaria byronia*).

Considering the strong sexual dimorphism that is characteristic of the Otariidae, the interspecific comparisons were performed separately for each sex.

For comparisons between developmentally analogous phases of different species the same methodology is applied. In addition, a linear model is fited to the complete ontogeny of each species and the dominant trend is compared between them by resampling methods too. All the interspecific comparisons are made using two species each run-time. The basic accost is to compare the angle between ontogenetic vectors of two species to angles between ontogenetic vectors from one species (the angle between the

[36] Where one trajectory is vertically transposed relative to the other.

vectors of two species would be considered distinct if it super pass that angle calculated from samples designed from one species).

Testing for channeling- To test statistically this hypothesis, we should check if perhaps exists a significant difference between the ontogenies of shape or in the shape at the youngest comparable phase. The initial shape[37] is estimated by the means of the specimens of age equal to zero years[38]. We expect to find only a difference in the length of the ontogenetic vector[39]. To perform this tests, we needed to measure angle between the (normalized) vector of allometric coefficients which were carried out by the estimation of the the angle and the correlation (cosine) between the mentioned vectors. The cosine of the angle is the inner product of vectors of allometric coefficients, normalized to unit length. So, it is possible to test the null hypothesis that the trajectory of shape is conserved during all the species ontogeny (when the angle between the vectors will be 0.0º the cosine will be 1) using a resampling procedure to obtain confidence intervals for the angles (EFRON & TIBSHIRANI, 1993). This is very important because treating this angle of 0.0° as a null hypothesis is unrealistically strict. The null hypothesis is that the angles between the ontogenetic phases are no larger than we would expect from the variation within a single phase but it is expect variation anyway; the question here is how much the uncertainty of the estimation of each trajectory (due to sampling) is so large that we cannot reject the null hypothesis of no difference in ontogeny of shape. Initially, we tested if the observed angle could have been originated by two independent samples from the same ontogenetic phase by estimating the distribution of angles that could be obtained from repeated sampling of the ontogeny of a single group. The expected shape at each size is estimated from the multivariate regression equation, and residuals are calculated for each individual. Consequently, each specimen gives a multidimensional set of residuals representing its deviation from the expected shape for its size. The complete set of residuals for each individual is bootstrapped (N=100) with replacement as an entire set, thereby preserving the covariance structure among variables. After that, a replica of the original data set is produced by the addition of the set of residuals to the expected shape for each given size. Then, two ontogenetic vectors are derived from a pair of these randomic sets and the angle between them is calculated. When the observed angle between phases exceeded the 95% confidence interval of the two within-phase ranges, the difference between the vectors of the two stages was considered statistically significant. Furthermore, the differences in the sample sizes of the ontogenetic stages we taken in account in the distribution of the randomized data sets (the bootstrapped datasets taken as references had comparable sample sizes). In this context, the two bootstrap sets formed from the group with the largest sample size agrees with the sample sizes of the two groups that were compared (what means that one bootstrap set has the larger sample size of the original group and the other has the smaller sample size of the other original group). In the other way, the two bootstrap sets formed from the data of the group with the smaller sample size both have that sample size because it is wrong to perform a bootstrap larger than the original data set. The comparisons among vectors were performed in VecCompare6 (IMP).

It is necessary to compare their shapes at the outset of the measured phase of development too, using a pairwise resampling-based F-tests (N=100)[40] and we measure the magnitude of the difference between them in terms of the Partial Procrustes distance. This analysis was done in Two-Group6h (IMP).

[37] Outset of ontogeny.
[38] Considering that in that developmental phase, the dimorphism is not yet present (see Chapter 1 for details).
[39] The parameter that measures the total amount of change undergone in each ontogeny over the observed phase.
[40] Stabilization criteria (ZELDTICH et al, *in press*.)

Using regression, we acquired the developmental equation of each species, which predicts the expected shape at each size. We predicted the mean shape for each species at age zero, and then add the residuals from the regression to the predicted form, yielding a sample of shapes at each stage. Of course, each individual specimen contributes with a single residual[41]. To compare shapes, we employed MANOVA, followed by a posteriori tests of pairwise differences between species, and we also examine the misclassification rate of a discriminant function. The statistical significance of the pairwise differences is tested by a resampling-based. The MANOVA was performed by CVAGen6j, which also yields the misclassification rate; pairwise F-tests were done in Two-Group. These programs, part of the Integrated Morphometrics Programs (IMP), were produced in Matlab6 (Mathworks 2000); compiled stand-alone versions running in Windows are freely available electronically at http:// www.canisius.edu/;sheets/morphsoft.html.

Finally, we compared the length of their ontogenetic vectors as estimated by the Procrustes distance between youngest and oldest comparable ages, but always in considering the context of the sexual dimorphism in the ontogeny. That parameter is a function of the duration of development and of the rate of shape change. To estimate this length we estimated the Procrustes distance between the average shape at the initial shape (mean shape at age zero years) and at maximum body size. We so placed confidence limits in it by bootstrapping, taking into account the variability among individuals at a common size and the uncertainty of the regression. Specifically, we calculated the residuals from the regression, drew them (with replacement) at random and added them to the expected shape, forming a bootstrap data set for each group. We then fit the same regression model to the bootstrapped sets and carried out the size correction on the bootstrapped sets, giving a bootstrap set for each species (that incorporates the uncertainty of the regression). These calculations were performed in DisparityBox, another freely available program in the IMP series.

Testing for changes confined to early or late morphogenesis- If changes occur solely in early morphogenesis, we expect that species would be shaped differently at the youngest comparable stage, but subsequently follow the same ontogeny of form, and to the same extent. To verify if only early development is labile, we can show that there is a significant difference in shape at the outset of the measured phase, but that any differences in later development are neither significant or large. Statistically, we would test the hypothesis of no difference in mean shape at the outset comparable stage, of an angle between trajectories that does not significantly exceed 0.0º and of no difference in lengths of the vectors, using the methodologies explained above.

In the same way, if all change occurred in late morphogenesis, we would not observe differences between them at the youngest comparable developmental stage but a notable difference in their ontogenies of shape[42]. Again, we would test statiscally the hypothesis of no difference in mean shape at the youngest comparable stage, of an angle that do not significantly exceed 0.0º and of no difference in lengths of the vectors.

[41] The deviation of that individual from the predicted shape.

[42] The length of the trajectory of late development is not an issue here because changes in length are due to differences in rate/timing, not to differences in morphogenesis, so we have drawn trajectories of the same length.

RESULTS

Descripiton of the ontogenetic trajectories- The ontogenetic trajectories of the three species curve because the rate of shape change in higher is the early development and decreases further (Fig. 2).

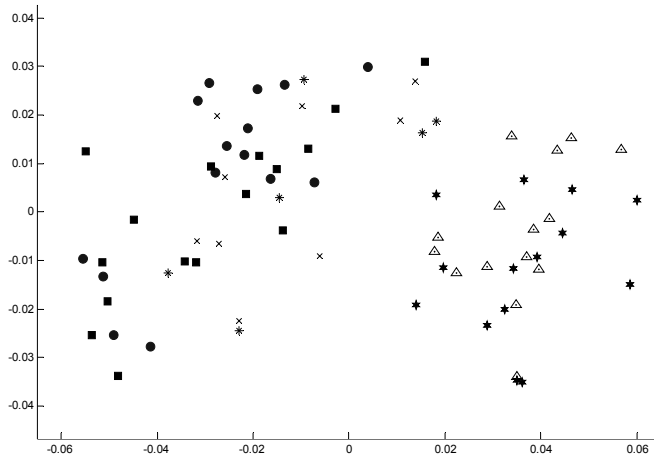
PC1 Describes the dominant linear trend, which accounts for near a half the variation in skull shape (43.69% in *Arctocephalus australis*; 42.20% in *Callorhinus ursinus* and 42.35% in *Otaria byronia*). The next PC describes age-related deviations from the linear trend. The second PC accounts for more that 12% of the variance in *A. australis* and the PC 3 explained about 6.4218%. In *Callorhinus ursinus*, the PC2 contributes with approximately 11.9% of the variance and the PC3 with 7.9253%. In *Otaria byronia* PC2 accounts for 9.43% and the PC3 for 7.6858%. In this species, it is remarkable that the ontogenetic trajectory of the females is more linear in comparison with the trajectory of the males (Table 2; Fig. 2).

But in all cases examined, only the first component is statistically distinct from the others principal components by the Anderson´s test. This is too the only PC that presents a significant linear relationship between its scores and age (absolute and sutural) and specially size (LogCS), a pattern shared by all species ($p< 0.01$) (Table 2). In the three otarid species, the correlation between the linear dominant trend in ontogeny is approximately uniform in magnitude. In contrast, the correlation with size is different[43] between them in slope and intercept ($p<0.001$) (Table 2).

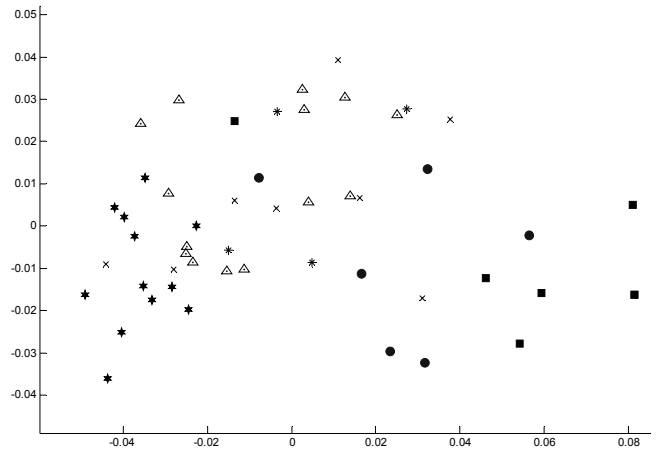
Table 2. Summary of the linear regressions results between the first Principal Component and absolute age and size (sex pooled together). The data working with sutural age are not presented here because they are less informative in this context.

	PC1 X AGE Correlation Coefficient	PC1 X AGE Determination Coefficient (R^2)	PC1 X LogCS Correlation Coefficient	PC1 X LogCS Determination Coefficient (R^2)
A. australis	0.605	0.366	0.85	0.72
C. ursinus	0.64	0.41	0.69	0.48
O. byronia	0.69	0.475	0.91	0.83

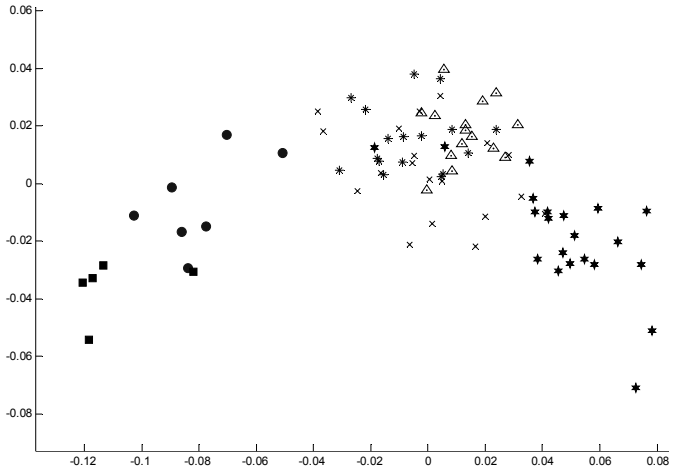
[43] *A. australis* and *C. ursinus* shows different slopes ($p<0.001$) and similar intercepts ($p=0.0531$). *A. australis* and *O. byronia* presents different slopes ($p<0.05$) and different intercepts ($p<0.001$). *C. ursinus* and *byronia* have similar slopes ($p=0.1252$) but different intercepts ($p<0.001$)



A



B



C

Figure 2[44]. Principal components analyses of shape pooling all specimens together. (A) *Arctocephalus australis*; (B) *Callorhinus ursinus*; (C) *Otaria byronia*. Circles=juvenile males,

[44] Note that the sign of the axis is arbitrary.

x=subadult males, stars= adult males, squares=juvenile females, asterisk= subadult females, triangles=adult females.

Observing the scatter plot of the 2 first principal components with all specimens pooled together, we notice that the rate of change in shape of *O. byronia* is smaller when compared with the other two species and that the PC1 contributes more with the variance in this species that in the other, what indicates a more longer ontogenetic trajectory. In both PC´s *C. ursinus* specimens present the smaller scores and *O. byronia* specimens the higher. Otherwise, we can observe that the juveniles of the later speciesare more differentiable (in respect of shape) from the other stages, than they are in the other species. The same can be observed in the adult males of this species (Fig. 3).

The PC1 (68.37% of the total variation) describe basically the growth of the rostrum and the enlargement of the braincase and of the zigomatic arch, more pronouncedly. The PC2 (8.5% of the total variation) describe the elongation of the splancnocranium and the deeper of the braincase, including the condyle region . The PC3 (4.14% of the total variation) represents de expansion in breath of the basicranium (Figs. 3 and 4). PC4 (3.51%) and PC5 (2.32%) are significantly different from the other ones too.

In the plot of the scores of the PC2 and the PC3, it is remarkable that the fur seals are condensed in a smaller region of variation in the PC2 (overall *C. ursinus*) during ontogeny and that the sea lions present the higher coefficients in the PC3. In that plot is very clear the correlation of the PC2 with ontogeny (the adults have the higher scores) and also with sex (the males have the higher scores in all species). Additionally, the adults of *A. australis* are perfectly separated from the rest in their disposition (higher scores in the PC2 and smaller scores in the PC3) and once a time the juveniles of *O. byronia* are very distinct from the overall.

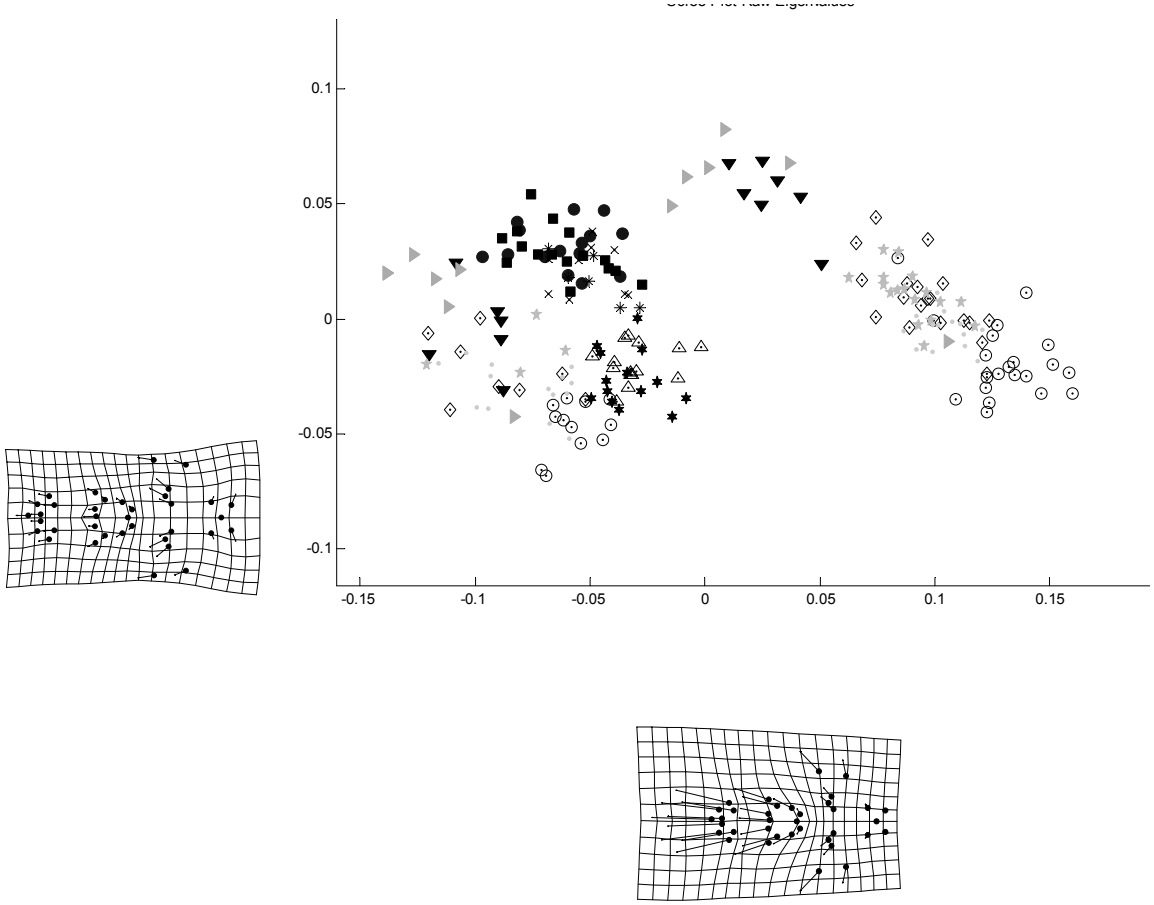


Fig 3. Principal components of shape. The difference between low and high scores on each axis (PC1 and PC2) is depicted as a Cartesian transformation by the thin-plate spline. Symbols for *A. australis*: Circles= juvenile males, x= subadult males, stars= adult males, squares=juvenile females, asterisks= subadult females, triangles= adult females; Symbols for *Callorhinus ursinus* and *Otaria byronia*: Reverted triangles: juvenile males, losangle=subadult males, "Circles with a point inside"= adult males, "triangles with a point inside"= juvenile females, gray stars= subadult females, small circles= adult females.

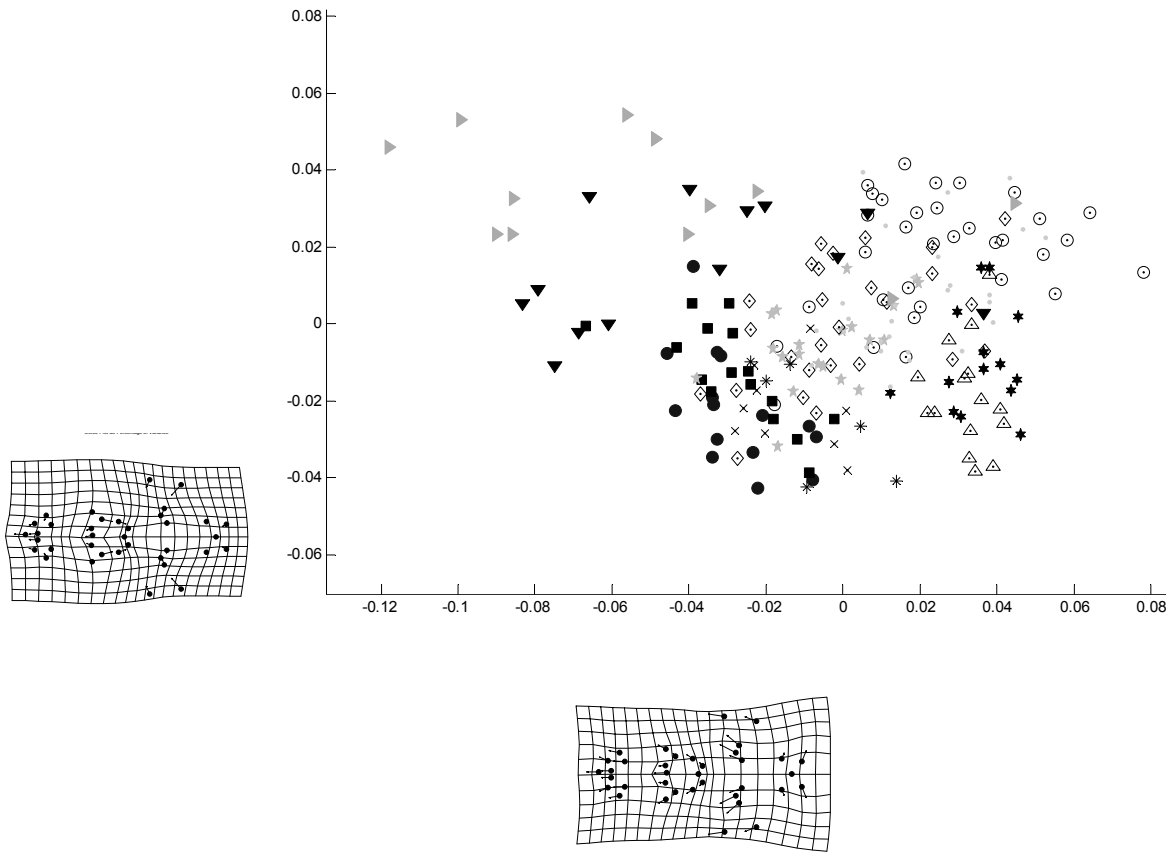


Fig 4. Principal components of shape. The difference between low and high scores on each axis (PC2 and PC3) is depicted as a Cartesian transformation by the thin-plate spline. Symbols for *A. australis*: Circles= juvenile males, x= subadult males, stars= adult males, squares=juvenile females, asterisks= subadult females, triangles= adult females; Symbols for *Callorhinus ursinus* and *Otaria byronia*: Reverted triangles: juvenile males, losangle=subadult males, "Circles with a point inside"= adult males, "triangles with a point inside"= juvenile females, gray stars= subadult females, small circles= adult females.

Patterns of shape change in ontogeny- When we performed the principal component analysis of the shape variables pooling the sexes separately, the percentage of variance explained for each PC is similar with the scenario described above for each species), but the ontogeny is less linear in the males that in the females (Table 3). The PC1 presents a higher correlation with size too ($p<0.05$), where the smaller value for R^2 is found in the females of *C. ursinus* (R^2= 0.7) and the higher value is found in the males of *O. byronia* (R^2=0.8357). Additonally, the PC1 is significantly correlated with absolute and sutural age for all subsamples of species/sex but the pattern of the relation between the other two PC´s (PC2 and PC3, which are taken together contribute for near of 20% of the variation generally) with age is complex and difficult to summarize (Table 3).

Table 3 . Amount of variance in shape explained by each of the first principal components in each species/sex group. The principal components significantly different from the others are labeled with an asterisk (*).

		PC1	PC2	PC3
A. australis	**FEMALES**	0.4836*	0.1130	0.0585
	MALES	0.4555*	0.1473*	0.0603
C. ursinus	**FEMALES**	0.4855*	0.1219	0.0791
	MALES	0.4011*	0.1385	0.1099
O. byronia	**FEMALES**	0.5288*	0.09	0.0818
	MALES	0.4603*	0.1167	0.0770

Observing the plottage of the scores in the two first PCs in each species/sex group, we can define the chronological point of inversion in the sign of the rate in most of the subgroups analysed (Figure 2). That point correspond to the age of 3 years (sutural age= 13 or 14) in the males of *O. byronia* and in the females of *A. australis* (sutural age=13-16) and to the age of 2 years for the males of *A. australis* (sutural age= 11-12) and for both sex in *C. ursinus* (sutural age of 12 and 15 respectively). In the females of *O. byronia* the pattern of the PCA plot is of low resolution and we could not identify the pattern of change in the rate of development in shape in our sample. Otherwise, the adults always constitute a defined group in the PCA plot, clearly separated from the imatures in any case. The same can be observed in the juveniles and in the adult males of *O. byronia*.

So, we can affirm that the ontogeny of shape in all subsamples of species/sex only can be described rigorously by a vector that curves multiple times in the space. In this context, we tried to documented the changing directions of the ontogenetic trajectories documented using the comparisons between the phases of ontogenetical stages (juveniles, subadults and adults).

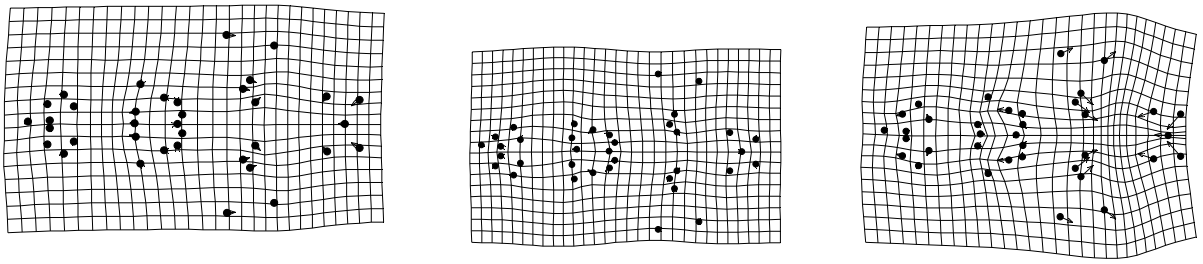
In the fur seals, we perceive larger and more significant differences between imatures and adults and in the sea lion the striking changes occurred in the early development, between the juveniles and the other groups. In addition, we show a significant difference between the allometries of adult males and adult females (Table 4, Figure 6). In the fur seals, juveniles and subadults are no more different that than expected by chance (what means that the correlation is not significantly different from 1). The same is true for the subadults when compared with the adult males. Contrasting, subadults and adult females are no more similar than expected by chance (the correlation is not statiscally distinct from zero), and the same is true for the comparison of the allometries between the different sexes (considering all specimens or only adults). On the other hand, only between subadults and adults of *O. byronia* the trajectories are no more different than expected by chance. These results are congruent with that obtained in the principal components analysis of ontogenies of shape and also in the comparisons of the mean forms between sexes.

Table 4. Comparisons between ontogenetic allometries of successive stages in the species studied. The angles are in degrees and the ones that are signed with an asterisk (*) are significant at the level of 5% (p<0.05).

A. australis				
datasets compared	**Between**	**correlation**	**within sample 1**	**within sample 2**
juveniles/subadults	23.7	0.915662593	51.6	39.8
subadults/adult females	**79.6***	0.180519145	64.7	76
subadults/adult males	66.6	0.397147891	70.7	55.3
adult females/adult males	**81.9***	0.140901232	78.7	53
C. ursinus				
datasets compared	**Between**	**correlation**	**within sample 1**	**within sample 2**
juveniles/subadults	18.3	0.949425478	35.1	35.9
subadults/adult females	**100.1***	0.175366726	37.2	67.6
subadults/adult males	52.8	0.604599115	76.3	63.2
adult females/adult males	**93.2***	0.055821505	82.8	68.4
O. byronia				
datasets compared	**Between**	**correlation**	**within sample 1**	**within sample 2**
juveniles/subadults	**76***	0.241921896	59.5	73.9
subadults/adult females	81.8	0.142628934	88.6	60.9
subadults/adult males	52.8	0.604599115	83.1	64.8
adult females/adult males	**66***	0.406736643	63.5	61

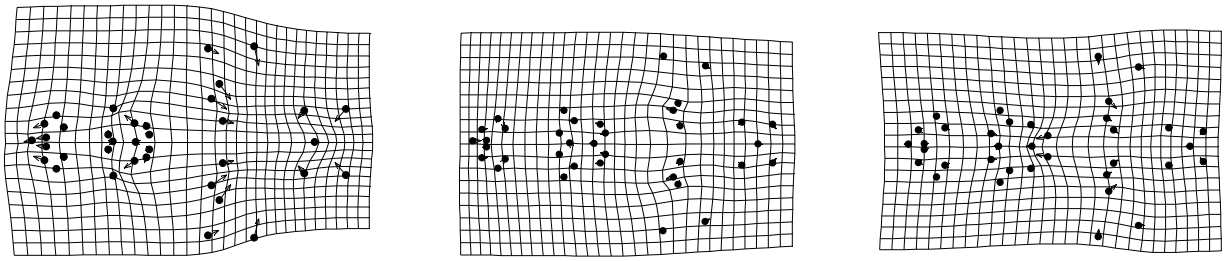
Arctocephalus australis

IMATURES **ADULT FEMALES** **ADULT MALES**



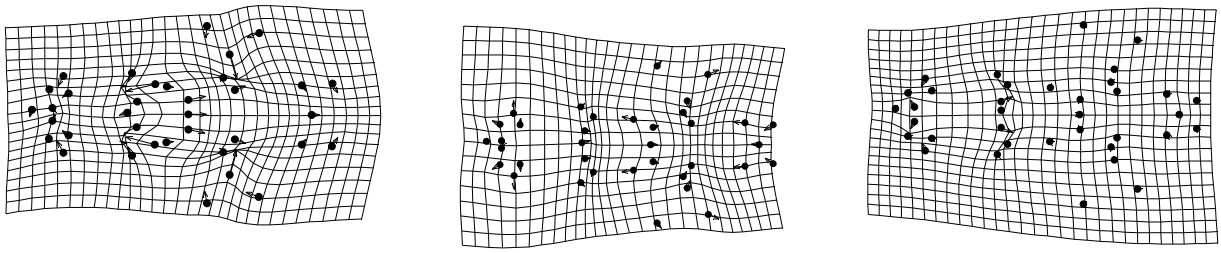
Callorhinus ursinus

IMATURES **ADULT FEMALES** **ADULT MALES**



Otaria byronia

JUVENILES **SUBADULTS** **ADULT FEMALES**



ADULT MALES

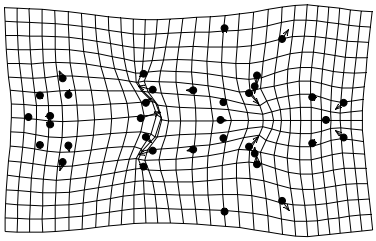


Figure 6. Stages in the ontogeny of shape in each species studied (only that ones that are statistically distinct from all others).

Comparisons between species when compared at a common size and age- The hypothesis that the mean shapes are the same is rejected at $P<2.22045e^{-016}$ for all tests (comparisons between species with each sex standardized at (a) the maximum value of the correspondent sex in the smaller species and (b) in the maximum value of the correspondent sex in the larger species and with each sex standardized at (c) mean shape at the age zero and (d) the mean shape at the age 10 years, totalizing 4 comparisons between the females of different species and 4 comparisons between the males of the 3 species considered). Different values of probability (but anyway hardly significant) were found for the second canonical variate for the comparisons between females standardized to the age of zero and 10 years, when $p=3.11219e^{-005}$ and $p=7.77156e^{-016}$, respectively. But in all cases there are two distinct Canonical Variates and the discriminant function classified the species always correctly. The first Canonical Variate distinguishes *O. byronia* from *C. ursinus* and *A. australis*. The second Canonical Variate distinguishes *C. ursinus* and *A. australis* (when *O. byronia* assumes an intermediary position in the scatter plot, more aligned with *A. australis*) (Figures 7 and 8).

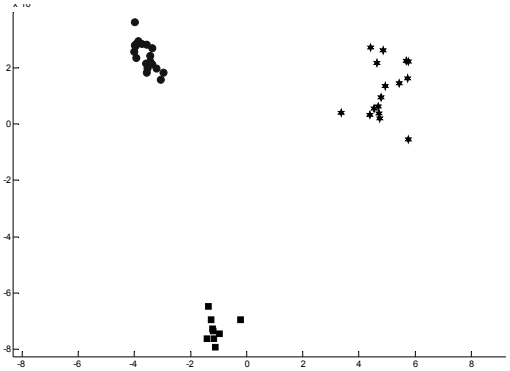


Fig 7. Scatter plot of the Canonical Variates of shapes of females standardized to the age of zero years. Circles= *Arctocephalus australis*, squares=*Callorhinus ursinus*, stars=*Otaria byronia*.

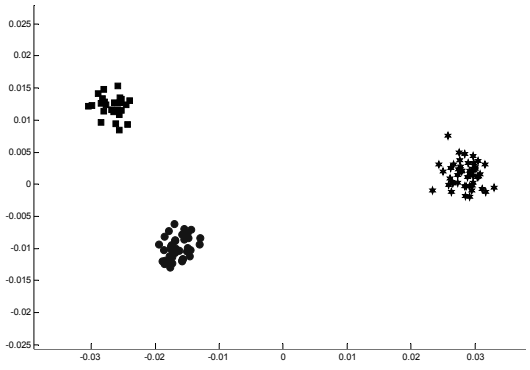


Fig 8. Scatter plot of the Canonical Variates of shapes of males standardized to the maximum size observed in the larger species (*O. byronia*). Circles= *Arctocephalus australis*, squares=*Callorhinus ursinus*, stars=*Otaria byronia*.

Considering the evidence of the scatter plot and the misclassification rate, it would not be necessary to test if each species differ significantly from the other but it is possible to ask by how much each differs (and if they differ from each other when compared at the same adult size than when compared at their actual adult sizes or yet if they are more or less different than that if compared at smaller/larger adult size of each species). The results are expressed at Table 5, where we observed that the difference is not simply an effect of extrapolating both to the relatively large size, but it is an important factor of influence.

Table 5. Partial Procrustes Distances between the species standardized for the same size or age in each sex. Confidence intervals at 95th percentile range are in parentheses. All distances are significantly different at p=0.01. Values in bold sign the Partial Procrustes Distances (PPD) that are significantly different from the PPD between samples standarized at the respective adult size. AA= *A. australis*, CU= *C. ursinus* and OB= *O. byronia.*

COMPARED SPECIES	SAMPLES STANDARIZED AT THE RESPECTIVE ADULT SIZE	STANDARIZED AT MAXIMUM SIZE *Arctocephalus australis*	STANDARIZED AT MAXIMUM SIZE OF *Otaria byronia*	STANDARIZED AT AGE OF ZERO YEARS	STANDARIZED AT AGE OF TEN YEARS
		FEMALES			
AA x CU	0.0733 (0.0656 - 0.0817)	0.0742 (0.0629-0.0837)	0.0882 (0.796-0.0959)	0.0795 (0.654-0.0964)	0.0807 (0.703-0.0968)
AA x OB	0.1454 (0.1404 - 0.1493)	**0.1288** (0.1235-0.1341)	**0.1866** (0.1793-0.1937)	**0.1139** (0.1037-0.1237)	0.1564 (0.1461-0.1705)
CU x OB	0.1911 (0.1825 - 0.1996)	0.1781 (0.1692-0.1875)	0.1866 (0.1793-0.1937)	0.1665 (0.1479-0.1830)	**0.1357** (0.1256-0.1480)
		MALES			
AA x CU	0.0594 (0.0520 - 0.0674)	0.0595 (0.0529-0.0674)	**0.0744** (0.0681-0.0836)	0.0747 (0.667-0.0860)	**0.0773** (0.0695-0.0888)
AA x OB	0.1712 (0.1650 - 0.1766)	**0.1483** (0.1434-0.1540)	0.1665 (0.1622-0.1715)	**0.1290** (0.1139-0.1409)	**0.1621** (0.1511-0.1701)
CU x OB	0.2093 (0.2004-0.2178)	**0.1868** (0.1783-0.1947)	0.2067 (0.1976-0.2149)	**0.1780** (0.1684-0.1929)	0.1943 (0.1837-0.2064)

The angles between the allometric vector bec0me significantly different from zero in the fur seals in the adult phase. The analysis of the ontogeny (in each sex or with sexes pooled together) is difficult to interpret due to the high angles within each species, suggesting a very large variation in the species ontogeny (Table 6) but a contrasting pattern was found when we compare the fur seals with the sea lion (Tables 7 and 8). On the other hand, when we compare the allometry pattern of *O. byronia* with *Callorhinus ursinus* we found that nearly all angles are significantly different from stages, except between the subadults (Table 8).

Table 6. Angles between allometric vectors of different ontogenetic stages of *Arctocephalus australis* and *Callorhinus ursinus*, estimated as the arc cosine of the vector correlation between ontogenetic vectors of partial warps normalized to unit length. The bold angles denote different allometries (p < que 0.05).

DATASETS COMPARED	Between	correlation	*A. australis*	*C. ursinus*
juveniles	48.5	0.66262	77.9	37
subadults	80.1	0.171929	85.3	72.3
adult females	**80**	0.173648	75.7	74.3
adult males	**77.6**	0.214735	69.8	72.6
overall	41	0.75471	24.3	52.8

Table 7. Angles between the ontogenetic vector between the ontogenetic stages of pairs of *Arctocephalus australis* and *Otaria byronia*, estimated as the arc cosine of the vector correlation between ontogenetic vectors of partial warps normalized to unit length. The bold angles denotes different allometries (p < 0.05).

DATASETS COMPARED	Between	correlation	*A. australis*	*O. byronia*
juveniles	60.1	0.498488	79.2	45.6
subadults	72.4	0.30237	76.1	87.2
adult females	**79.5**	0.182236	69.7	31.5
adult males	67.2	0.387516	58.5	68.5
overall	**38.7**	0.78043	16.1	15.9

Table 8. Angles between the ontogenetic vector between the ontogenetic stages of pairs of *Callorhinus ursinus* and *Otaria byronia*, estimated as the arc cosine of the vector correlation between ontogenetic vectors of partial warps normalized to unit length. The bold angles denotes different allometries (p < que 0.05).

DATASETS COMPARED	Between	correlation	*C. ursinus*	*O. byronia*
juveniles	**63**	0.4539905	52.5	48
subadults	88.6	0.02443218	71.9	90.1
adult females	**105.8**	0.2722802	71.3	30.8
adult males	**78.1**	0.20620419	66	68.3
overall	**40**	0.76604444	23.9	19.7

DISCUSSION

C. ursinus is always more in agree with *A. australis* and more disparated from *O. byronia*. Size have a strong relevance in the explanation for that fact, but the shape (such as the morphogenesis of the splancnocranium) is equally important. The PPD is also coeherent with the phylogeny. The difference in mean shape between any of the fur seals is always larger than the difference between them, overall in the males. Additionally, the shape distances between species increase during ontogeny without a strong influence of size; attaining the maximum in the adults, which is in agreement with the pattern exhibited in the PCA plot too.

Generally, a different pattern is found between fur seals and sea lion in the ontogenetic parameters (e. g. pattern of the direction of the allometric vectors and length of the trajectory). But for all species, the changes are more intense in the imatures (except in *A. australis*) and in the adult males (what could be related to the secondary growth, related to the secondary sexual dimorphic characters linked to the development of the muscles). In *O. byronia*, the ontogeny is less linear, with more significantly different pattern in terms of allometry.

The relevance of size to determine the difference between the species is obvious in our results and coherent with the relation with sex and size also. Thus, when we standardize the samples to smaller size (like the larger size observed in *A. australis* or mean size of each species at zero years) the differences in shape between the females of *A. australis* and *O. byronia* and between the males of the fur seals and the sea lion decrease. On the other hand, when the samples were standardized to a large size the differences between the fur seal females and sea lion females decrease (standardized to the maximum size of the larger species – *O. byronia*) and the differences between the fur seals males increases (standardized at the mean size of each species at 10 years old).

We can conclude that the skull morphogenesis of the otarids examined is a dynamic and complex process in all parts of the skull of all species. The trajectories of skull morphology curve over ontogeny in all the examined species. Thus, empirically, issues are rather more complex than suggested by the heuristic diagrams presented in ALBERCH et al. (1979). But it is in their very complexity that these trajectories provide a basis for exploring changes in the spatial distribution of developmental processes (ZELDITCH et al., 1992). Whether ontogenetic trajectories are linear or curve could be a function of developmental timing or more specifically it could depend on the age at which allometries stabilize in post-natal ontogenies. Treating ontogenetic trajectories as ontogenetically and historically constant simplifies comparisons, but it obviously implies in loss of information about the ontogenetic and evolutionary dynamics of morphogenesis (ZELDITCH et al, 2003b). Considering that our results deviate from a linear model in the ontogeny it would be problematic to perform a heterochronic analysis. But allometric repatterning surely can be observed in the results here presented because we perceived modifications in the pattern of ontogenetic shape change between the species.

The distinction between allometric repatterning and heterochrony is that when we verified heterochrony, we observe a conservation of the ratios between the allometric coefficients, which is not verified in allometric repatterning (the ratios of the allometric coefficients are modified during the trajectories) (Miriam Leah Zelditch, personal communication).

MacNAMARA (2002) argues, about the work of ALBERCH et al., 1979: "*By including rate changes they effectively negated parallelism as a factor in heterochrony. The consequence of changing rates of*

development of organs or structures was to change allometries, thus removing any direct parallelism between ontogeny and phylogeny. Changing ontogenetic trajectories in this way mean that a descendant´s ontogenetic pathway would be different from that of its ancestor." (MacNAMARA, 2002:551). But the question is not to maintain the rate of the trajectory but it is to conserve the same ratio between the allometric coefficients. Thus, changes in rates between ancestor and descendent is not an issue, but if we intend to test for heterochrony, it is important that the ontogeny of each species does not present modification in rate between ages of the same trajectory. Clearly, heterochrony is not synonymous of ontogenetic scaling. It is possible to document heterochrony with a decoupling of growth form and development (but only those consistent with the hypothesis that morphogenesis is conserved) (ZELDITCH, *in press*).

PCI shows the dominant linear ontogenetic, but there is a substantial deviation from linearity, evident by the fact that PCII is also age-related. This pattern is similar between the species. There is no easy way to transform these data, and it may be inadvisable to do so anyway because the dynamics of that trajectory are not just a nuisance—they are biologically interesting. But they certainly do complicate comparative analyses because we need to decide which biologically comparable vectors are before we can make meaningful comparisons. Treating ontogenetic trajectories as ontogenetically and historically constant undoubtedly simplifies comparisons, but that simplicity has a high cost – loss of information about the ontogenetic and evolutionary dynamics of morphogenesis. Some workers have questioned whether those ontogenetic and evolutionary dynamics pose serious problems for studies of heterochrony (PENIN & BERGE, 2002). Our results indicate that the deviations from a simple linear model are substantial in ontogeny, which difficult a comparaison in terms of ontogeny and phylogeny (the rates of changes changes between ontogeneetical stages of each species so, it is very complicated to compare rates between species of a phylogeny).

When we are evaluating the role of development in evolution dissociation we get a productive notion to base an understanding of the interrelationships between developmental and evolutionary processes. But when we are evaluating the role of development in evolution, we can find heterochronies causing evolutionary change, but we also can find heterochronies arising as incidental results of other dissociations. If we do not make that distinction, we risk robbing the concept of heterochrony of explanatory power by uncritically ascribing all morphological change to it (RAFF & WRAY, 1989). It is possible that heterochrony is so common only because it has been the focus of concerted attention for two decades, whereas the hypothesis of heterotopy[45] is rarely even considered, much less tested. Also, some workers have expanded the definition of heterochrony to the point that virtually any evolutionary change in the ontogeny of form would be qualify as heterochrony (e.g., MCKINNEY & MCNAMARA, 1991).

We are not ignoring the possibility of dissociated heterochrony, but the question here is that any part of the skull of the otarid studied seems to evolve by a simple truncation or extrapolation of a shared ontogenetic trajectory. The proportions within the regions are altered, so it does not appear that any one is simply pedo or peramorphic). Growth rates have a location and spatial organization, not only a magnitude, and there is not logical good reason to suppose that spatial aspects of growth are conserved while temporal parameters evolve.

In the presente study, taxa differ in relative growth rates for different features, so these within-sample components describe different shape changes and the PC1 cannot be regarded as a homologous feature.

[45] A concept that can be applicabe only to ontogenetically static morphological features (ZELDITCH, personal communication)

When taxa diverge in shape correlates of size, there is no common ontogenetic shape axis on which to compare them.

Heterotopy should be applicable only to ontogenetically static morphological features. If the structure undergoes migration during ontogeny, then an evolutionary difference in location of the structure may alternatively be interpretable in terms of temporal modification of the migratory path, and/or in terms of repatterning[46] of the migratory pattern.

Heterometry and heterotopy are distinct from allometric repatterning in that they describe modification of the number and spatial distribution of ontogenetically static structures on the organism. Allometric repatterning describes the dynamics of shape change through ontogeny. Of course, hetrotypy, heterometry, or hetrotopy in local morphological structures can have a "shunting" effect resulting in modification to shape on a more global scale. If allometric repatterning on one scale is to be fully accounted for by such processes on a more local scale, then it should be possible to demonstrate conservation of ancestral patterns of ontogenetic shape change at that local scale, subject to dimensionality bias. Whether and how shape data are treated is the primary cause of dimensionaly bias. The bias therefore impacts the ability to identify allometric repatterning and to distinguish this from alternative modes of ontogenetic modification. Heterochrony and allometric repatterning are therefore mutually exclusive caegories when assessed for the same morphological structure. Where a particular phase of shape change in the descendent is modified in both temporal and spatial aspects with respect to the homologous phase of development in the ancestor, then allometric repatterning with rate/timing modification has been demonstrated. However, the degree to which taxa aredetermined to share the same trajectory of ontogenetic shape change depends on the complexithy with which shape is summarized. Shape is inherently multidimensional, and trajectories of shape change must therefore be quantified utilizing multidimensional vectors (ZELDITCH et al., 2000). Heterochrony detected in such a way is an artifact of the geometric constraint imposed on the data: one dimensional data are constrained in that taxa can differ only in terms of the point at which progress along that dimension starts or stops, or in the rate of progress along that dimension. Simplifying shape description (or restricting morphological coverage to more localized regions to test for heterochrony on a local scale) often decreases the number of shape variables and the dimensionality of the analysis, thereby increasing the probability of detecting rate or event heterochrony to a virtual certainty.

The study of change in mean form from age to age is only a first step in relating ontogeny to morphological evolution. It is the variation among individuals in these features of skull growth, and the covariation among phases growing features, that influence how skull shape evolves (ZELDITCH et al., 1992).

Sometimes, heterochrony is defined so broadly that it means nothing more than that ontogeny evolves. That broadly defined, heterochrony refers neither to particular pattern nor to a class of phenomena that share a cause (ZELDITCH et al. *in press*). The search for a method whitch will possibilite the quantification and comparisons between trajectories in a multicimensional space should be considered seriously in futures researches.

[46] About allometric repatterning: modification in the pattern of ontogenetic shape change-ancestor and descendant differ in the trajectory of ontogenetic shape change followed by a structure of the organism. The parameter of interest is the pattern of shape change followed by a structure or individual over a specified ontogenetic interval. The distinction between allometric repatterning and heterochrony lies their different impacts on ratios among allometric coefficients: in the case of heterochrony these ratios are conserved across the taxa, but in the case of allometric repatterning they are modified.

APENDIX 1. ANATOMICAL DESCRIPTION OF THE LANDMARKS

1- anteriormost point of the pré-maxilla tuberosity
2- antero-lateral extremity of third incisive alveolus
3- anteriormost point of incisive foramen
4- lateral extremity of canine alveolus
5- anteromedial point of first post-canine alveolus
6- anteriormost point of the maxilla-palatine suture
7- point that label the direction change of the maxilla-palatine suture
8- posteriormost point of the root at the lateral limit at bone palate of zigomatic process of the maxilla
9- posteriormost point of sixth post-canine alveolus
10- posteriormost point of palatine extension of maxilla (“pterygoid” process of the maxilla)
11- posteriormost point of interpalatine suture
12- point that label the direction change of the posterior border of palatine
13- posteriormost extremity of oval foramen
14- lateral extremity of jugal-esquamosal suture
15- medial extremity of the contact between the glenoid fossa and the ectotympanic
16- anteriormost extremity of the anterior aperture of carotid canal
17- antero-lateral corner of mastoid process
18- posteriormost point of the condiloid foramen
19- posteriormost point of occipital condyle
20- anteriormost point of foramen magnum.

CAPÍTULO V

THE ONTOGENY OF SHAPE DISPARITY IN THREE SPECIES OF OTARIDS (PINNIPEDIA: MAMMALIA)

THE ONTOGENY OF SHAPE DISPARITY IN THREE SPECIES OF OTARIDS (PINNIPEDIA: MAMMALIA)

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ABSTRACT

Variation and disparity are similar terms related to the concept of variety where disparity signifies generally the variety among groups, being the outcome of evolutionary processes and variation is the variety of individuals within a homogeneous group, being the raw material to the evolutionary processes. The objective of the present work is to compare ontogenies to identify novelties in the skull shape of otarid species to understand their relationships with the diversity. The species studied were *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*. We analyzed evolutionary changes in three parameters of developmental trajectories of skulls shape: shape at the outset of ontogeny, allometric pattern and the amount of change undergone over the course of ontogeny, which depends on the duration (the length of the ontogenetic vector) and rate of development. Initial shapes are always very different among the species and the distances between shapes increase with time independently from size. Furthermore, when the complete samples are considered, all the ontogenetic trajectories are significantly different in which concern the directions of the allometric vectors during ontogeny. Ontogenetic trajectories differ significantly among almost all the pairs compared, except for the trajectories of *A. australis* and *C. ursinus* males. They are no more different than expected by chance considering the range of angles within each sample. A similar pattern is found when the subadults are compared between pairs of species and when we compare adult males of *A. australis* with adult males of *O. byronia*. The juveniles are no more different than expected by chance (correlation between ontogenies in that phase is equal to one), excepting between *C. ursinus* and *O. byronia*. The ontogenetic trajectory of *C. ursinus* is the shorter and of *O. byronia* is the longer being near the triple of the former. *A. australis* has an intermediary length of ontogenetic trajectory. For the sample comprising all three species disparity increase significantly over ontogeny since the disparity of the adults is near the double of the disparity between juveniles. For any ontogenetical stage, *O. byronia* is the species that more contributes for the disparity of the group, followed by *C. ursinus*. When we consider the three species together, the pattern of disparity do not change a lot during ontogeny. Ontogenies examined herein are clearly not constrained and perhaps the differences in patterns have additive effects in the differentiation of the ontogenies.

INTRODUCTION

Disparity and taxonomic diversity provide insight into the expansion and contraction of variety and the relationship between these two aspects of diversity, and also have important implications for evolutionary mechanisms. Disparity is measured as the total variance among forms in morphological space (proportional to the mean squared distance among forms) (FOOTE, 1993). This quantity is a measure of the range of morphologies in a given sample of organisms, as opposed to diversity, which is expressed in terms of the number (and sometimes ranking) of taxa.

The concept of biological and ecological diversity is a familiar one. It can be assessed by a variety of indices, usually dependent upon the number of taxa present in a given sample. A related concept is the absolute morphological variety of a group, its variance in form or the amount of morphological space that it occupies (FOOTE, 1992). The concept of disparity refers to members of a group of organisms under consideration are morphologically different from each other, then geometric morphometry provides a very objective assessment for these differences (FOOTE, 1992).

Furthermore, Variation and disparity are similar terms related to the concept of variety where disparity generally meansthe variety among a group. It is the outcome of evolutionary processes and variation is the variety of individuals within a homogeneous group. It is the raw material to the evolutionary processes (ZELDITCH et al. *in press*).

The objective of the present work is to compare ontogenies to identify divergent developmental feataures in the skull shape of the otarid skull with the purpose of understanding their relationships with diversity. The species studied were *Arctocephalus australis*, *Callorhinus ursinus* and *Otaria byronia*. We present a comparative study of the ontogeny of the skull of the two Otariidae species more frequent in the coast of Rio Grande do Sul State, Brazil (*O. byronia* and *A. australis*). *Callorhinus ursinus* is also included because it is supposedly the extant otarid more closely related to of the ancestral of this family. In this context, we analyzed evolutionary changes in three parameters of developmental trajectories of shape of skulls: (1) shape at the outset of ontogeny, defined here as the starting point of the vector representing the ontogeny of shape; (2) allometric pattern or, the direction of allometric vector in shape space and (3) the amount of change undergone over the course of ontogeny, which depends of the duration (the length of the ontogenetic vector) and rate of development.

That approach is justified by the fact that the study of disparity is primordial step to understand how evolutionary novelties interact in that groups which is particularly interesting considering the rapid (and poorly understood) radiation and speciation of the extanct Otariidae.

Then, the shape disparity between different developmental stages is compared. A decrease in the disparity level during ontogeny besides presence of novelties could indicate that novelties, perhaps, could reduce disparity due to the interactions non-addictive (ZELDITCH et al., 2003a).

The selected focus was skull shape because ontogenetic series of shapes are easily available and still because shape data are especially well suited to studies of disparity (ZELDITCH et., 2003a). Shape underlies the general statistical theory of modern shape analysis, the Procrustes distance. If in one side, traditional morphometrics presents a major analytic problem caused by discrete characters, which is that units of the same apparent magnitude are not necessarily equivalent (ZELDITCH et al. op cit.). However, any two samples that are separated by one unit of Procrustes distance differ from each other by the same amount as any other taxa that differ by one unit of Procrustes distance. That aspect is important when we objective to quantify the degree of difference among morphologies, overall when it concerns non-additivity of the interacting causes of disparity. Otherwise, this distance can be traced directly to the modifications in the place of homologous landmarks—the change in those locations is directly proportional to the difference in shape (ZELDITCH et al., 2003a).

MATERIALS AND METHODS

Sampling- Our samples comprise cross-sectional ontogenetic series of skull of three otarid species: *A. australis* (n=76), *C. ursinus* (n=51) and *O. byronia* (n=84). We use the number of growth layer groups deposited in the dentine of the bisected canine as our estimate of chronological age (SCHIAVINI, 1992) and the sutural ages to determine the ontogenetic stages (juvenile, subadults and adults) (SIVERTSEN, 1964). The analyses were performed considering species, sex, sutural age groups (Juveniles, subadults and adults).

Our analyses are based on landmarks, discrete points that are recognizable and homologous on all species and specimens of different ages in the study (Fig. 1).

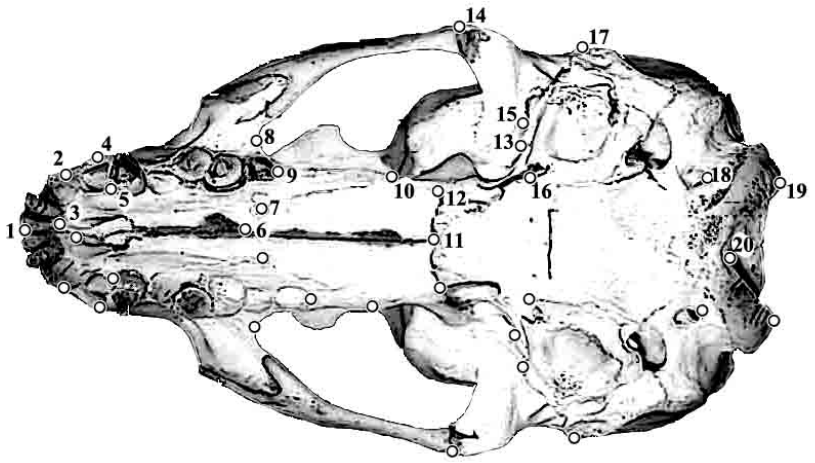


Figure 1. Landmarks shown on the skull of a juvenile of *O. byronia*. Descriptions of each landmark are given in Appendix 1.

The landmarks were chosen to provide the most comprehensive coverage of that view of the skull. Consistency of relative position, repeatability and coplanarity of the landmarks were also considered in the selection of the landmark points. All landmarks were digitalized by one of the authors (D. Sanfelice). The specimens were superimposed using the Generalized Least-Squares Procrustes superimposition (GLS).

Defining Morphological space and measuring morphological diversity – the approach here is to ordinate forms in a multidimensional morphospace and to base morphological differences, on the array of points in morphospace (CHERRY et al. 1982). Consequently, disparity is measured as the sum of univariate variances of all dimensions in morphospace, which is proportional to the mean squared Euclidean distance among points in morphospace (VAN VALEN, 1974).

The partial disparity is analogous to a variance, where the squared distances are taken relative to the overall centroid rather to the centroid of the subgroup. It permits the access to the disparity contributions of subgroups. This has allowed morphological disparity analysis to address an issue that has long been addressed with taxonomic diversity data, that concerning the relative contributions of different subgroups to overall morphological disparity. The method of disparity partitioning allows an assessment of the relative contributions of different taxa to the mophological disparity of the larger group containing them.

Comparisons of the Allometric Trajectories - These parameters were assessed by multivariate regression of the partial warp plus the uniform component scores (dependent variable, representing shape) on a measure of geometric scale (the logarithm of the centroid size). For each species separately, the full set of shape variables was regressed on the independent variables considered. We assume a linear relationship between shape and size since these estimates are based on linear regression.

Estimation and Comparisons among the Initial Shapes - The initial shape is estimated from the regression equation, which predicts the expected shape at each size or age. Here, we predict the mean shape for each species at age zero. The sexes were pooled together considering that the juveniles are not dimorphic in shape. After that, the residuals from the regression were added to the predicted form, yielding a sample of shapes at each stage. Each individual specimen contributes with only one residual—(the deviation of that individual from the predicted shape). To compare shapes, multivariate analysis of the variance (MANOVA) was performed and pairwise comparisons tested the differences between the groups two-by-two.

The misclassification rate of the discriminant function was analyzed too. The statistical significance of the pairwise differences was tested by a resampling-based *F*-test. The MANOVA and the misclassification rate was performed by CVAGen6j; pairwise *F*-tests were done in Two-Group6h. These programs pertain to the Integrated Morphometrics Programs (IMP), writen by D. H. Sheets and freely available electronically at http://www.canisius.edu/;sheets/morphsoft.html.

Estimatives and Comparisons between Allometric Patterns - The vector of allometric coefficients that describes morphogenesis is calculated using again the multivariate regression of shape on size, as detailed anteriorly. To compare these vectors multivariately, we calculated the angle between them and the cosine of that angle is the vector correlation between the two ontogenetic trajectories of shape. That cosine is calculated as the inner (dot) product of vectors of allometric coefficients, normalized to the unit length. So, if two vectors point in the same direction, the angle between them would be equal to zero and the cosine would be 1.0. However, to consider the angle of 0.0 as the null hypothesis is really too strict , but the null hypothesis is that the angles between species are no larger than we would expect from the variation within a single species or group (some variation is expected because individuals of the same species do not have identical ontogenies of shape). The subject here is whether the uncertainty of the estimation of each species trajectory (due to sampling) is so large that it is not possible to reject the null hypothesis of any significant difference. To estimate the range of angles within each species in congruence with the datasets, and thus to calculate the imprecision of the trajectory due to sampling, we estimate the residuals from the multivariate regression such that each individual gives a multi-dimensional set of residuals describing its deviation from the expected shape at its size. In this way, a pair of bootstrap sets was constructed for species and they will be used to calculate the angle between the trajectories in consideration. These pairs are constructed by resampling residuals (with replacement) and randomly assigning them to expected values of shape (derived from the original regression model) at values of the logarithm of centroid size detected in the original data. This bootstrap approach is no more than a multivariate extension of the known procedure to estimation of uncertainties of regression slopes by resampling the covariance structure among variables (EFRON AND TIBSHIRANI, 1993). Finally, the angles between the trajectories derived from the two within-species bootstrap sets are estimated and this procedure is repeated *N* times to produce a distribution of within-species angles. In the present study, we employed *N*=100. Because the sample sizes are different among the species, the two bootstrap sets constructed from the species with the bigger sample size match the sample sizes of the two species in comparison (that means, one set has the larger sample size of that species, the other has the smaller sample size of the other species). The two bootstrap sets formed from the data of the species with the smaller sample size both have that sample size, because it is not correct to construct a bootstrap larger than the original data set. Should the interspecific angle exceed the 95th percentile of the within-species range of angles, the interspecific difference is so considered to be statistically significant. The multivariate regressions are done using Regress6k and the comparisons between ontogenetic trajectories are done using Vec-Compare, both freely available programs in the IMP series.

Estimations and Comparisons between the Lengths of Ontogenetic Trajectories - The length of the ontogenetic trajectory of shape is a function of the rate of shape change and the duration of development. To estimate this length, the Procrustes distance between the average shape in the juvenile stage and the shape at maximum body size is calculated. Confidence limits are placed on this measure by bootstrapping, considering the variability among individuals at the same size and the uncertainty of the regression. That is, the residuals estimated from the regression are drawn with replacement at random and

added them to the expected shape, forming a bootstrap data set for each species. In the sequence, the same regression model was fitted to the bootstrapped sets and the size correction was carried out on the bootstrapped sets. The result was a bootstrap set for each species that incorporated the uncertainty of the regression. These calculations were done by DisparityBox6g, another freely available program in the IMP series.

Measurement of the Level of Disparity - The level of disparity is calculated in agreement toZELDITCH et al (2003a). To test the significance of differences in levels of disparity, we used the bootstrapping procedure explained in the previous section because the analyses presented here are based on standardized data and the tests should consider the uncertainties of the regression. When placing confidence intervals on disparity, we removed individual specimens but not to are into account the intraspecific variability. Considering that one of the difficulties found in calculating the level of disparity are the differences in shape related toh differences in size (allometry) and its influence in the disparity, the level of disparity was studied without and with correction for size. That means that we fitted a regression model to the data, determining the residuals and produzing size-standardized data set. In this context, we measured the disparity with and without correction for size. In the last case, we measured disparity with correction to the mean size of each subsample and with correction using the same size for the two samples. In addition, the Partial Disparity, that is the contribution to disparity of each subsample analyzed was calculated using Disparity Box6g (IMP series).

Analysis of the Pattern of Disparity - The dimensions and the distribution of shapes along the series where shapes are most disparate as described by principal components analysis, using the softweare PCAGen6n (IMP series). Such examinations are relevant because distinct ontogenetic stages might have the same level of disparity but present a different pattern, which hide the dynamic nature of disparity (ZELDITCH et al. 2003b). The patterns are examined for each subsample separately with the aim of find one biological explanation to the direction of dominant variation within shape space besides the fact that the morphospace resultant is different from sample to sample. The significance of the principal components was tested by the Anderson´s test.

The sub-samples compared were: juveniles (specimens with sutural age between 9 and 10, including newborn and animals between 0 or 1 year old), subadults (specimens with sutural ages between 11 and 18) and adults (specimens with sutural ages superior to 18), but the adults are separated by sex, due to the dimorphism in the adult shape. The method employed to the determination of the sutural ages is described in SIVERTSEN(1954).

RESULTS

Comparisons among the Initial Shapes –All pairwise F-tests among species show statistically significant differences in the initial shape (p=0.01), even after Bonferroni corrections for 3 comparisons. In addition, no specimens (n= 47) were classified incorrectly by the discriminant function. The pairwise distances between means are presented below (Tables 1 and 2), suggesting lability in the initial shape of the otarid skull shape.

Table 1. Procrustes distances between the average initial shapes. All pairwise differences are statiscally significant at the Bonferroni-adjuste value of α=0.05.

	A. australis	*C. ursinus*	*O. byronia*
A. australis	0	0.0685	0.1003
C. ursinus		0	0.1444
O. byronia			0

A. australis x C. ursinus	**DISTANCE**	**95% IC**	**ST. MINIMUM**	**95% IC**
JUVENILES	0.0685	0.0577-0.0861	0.0719	0.0628-0.0821
SUBADULTS	0.0647	0.058-0.08	0.0592	0.0551-0.0674
ADULT FEMALES	0.0673	0.0552-0.0793	0.0543	0.0478-0.065
ADULT MALES	0.0497	0.0444-0.0567	0.0573	0.909-0.1153
A .australis x O. byronia	**DISTANCE**	**95% IC**	**ST. MINIMUM**	**95% IC**
JUVENILES	0.0996	0.930-0.1125	0.1063	0.0989-0.1233
SUBADULTS	0.1444	0.1353-0.1528	0.1373	0.1299-0.1464
ADULT FEMALES	0.1387	0.1288-0.1459	0.142	0.1345-0.1488
ADULT MALES	0.1683	0.1578-0.1795	0.1662	0.1532-0.1747
C. ursinus x O. byronia	**DISTANCE**	**95% IC**	**ST. MINIMUM**	**95% IC**
JUVENILES	0.1445	0.1355-0.1566	0.1406	0.1356-0.1487
SUBADULTS	0.1842	0.1683-0.1989	0.16	0.1491-0.1703
ADULT FEMALES	0.1859	0.1747-0.1969	0.1717	0.1615-0.1807
ADULT MALES	0.1921	0.1839-0.2014	0.1745	0.1652-0.1841

Table 2. Procrustes distances between the average shapes. All pairwise differences are statiscally significant at the Bonferroni-adjuste value of α=0.05. Distance is the Partial Procrustes Distance; 95% IC is the confidence interval; st. minimum is the PPD when the samples were standardized to the respective smaller size.

Performing the same analysis for the other ontogenetic phases, we detect that the differences tend to increase during ontogeny and that size do not change a lot the amount of difference. In effect, we compare shapes with different standardizations (e. g. standardized for the minimum size of all specimens, for the maximum size of all the females, for the maximum size of all the males, for the range of size of the females of each correspondente species or yet, standardized for the range of size of the males of each correspondent species).

Allometric Patterns – When the complete samples are considered, all the ontogenetic trajectories are significantly different in what concerns the directions of the allometric vectors during ontogeny. Here, the allometric patterns of each sex are presented separately once a time the patterns are distinct between males and females of the same species. Ontogenetic trajectories differ significantly among almost all the paisr compared, except for the trajectories of *A. australis* and *C. ursinus* males. They are no more different than expected by chance considering the range of angles within each sample (Table 3). A similar pattern was found when the subadults were compared between pairs of species and when we compare adult males of *A.*

australis with adult males of *O. byronia*. The juveniles are no more different than expected by chance (correlation between ontogenies in that phase is equal to one), excepting between *C. ursinus* and *O. byronia*. The range of the angles is from 38.2° and 40.7° in females and from 38.1° to 48.8° in males. The more divergent trajectories found are those of *C. ursinus* and *O. byronia* in both sexes.

Table 3. Comparisons between ontogenetic trajectories. Vector correlations (Rv) are above the diagonal, angles (in degrees) are below the diagonal. Angles statistically significantly different from 0.0° are in bold.

FEMALES			
	A. australis	***C. ursinus***	***O. byronia***
A. australis	-	0.766044	0.785857
C. ursinus	**40**	-	0.758134
O. byronia	**38.2**	**40.7**	-
MALES			
	A. australis	***C. ursinus***	***O. byronia***
A. australis	-	0.772734	0.786935
C. ursinus	39.4	-	0.658689
O. byronia	**38.1**	**48.8**	-

It is possible to perceive thus that the three species examined are more similar than expected by chance (i. e. the correlation is higher than zero) but they differ significantly (i. e., the correlations are lower than 1). Additionally, the differences in the ontogenetic transformations of shape are visually conspicuous between sexes and overall between species (Fig. 2).

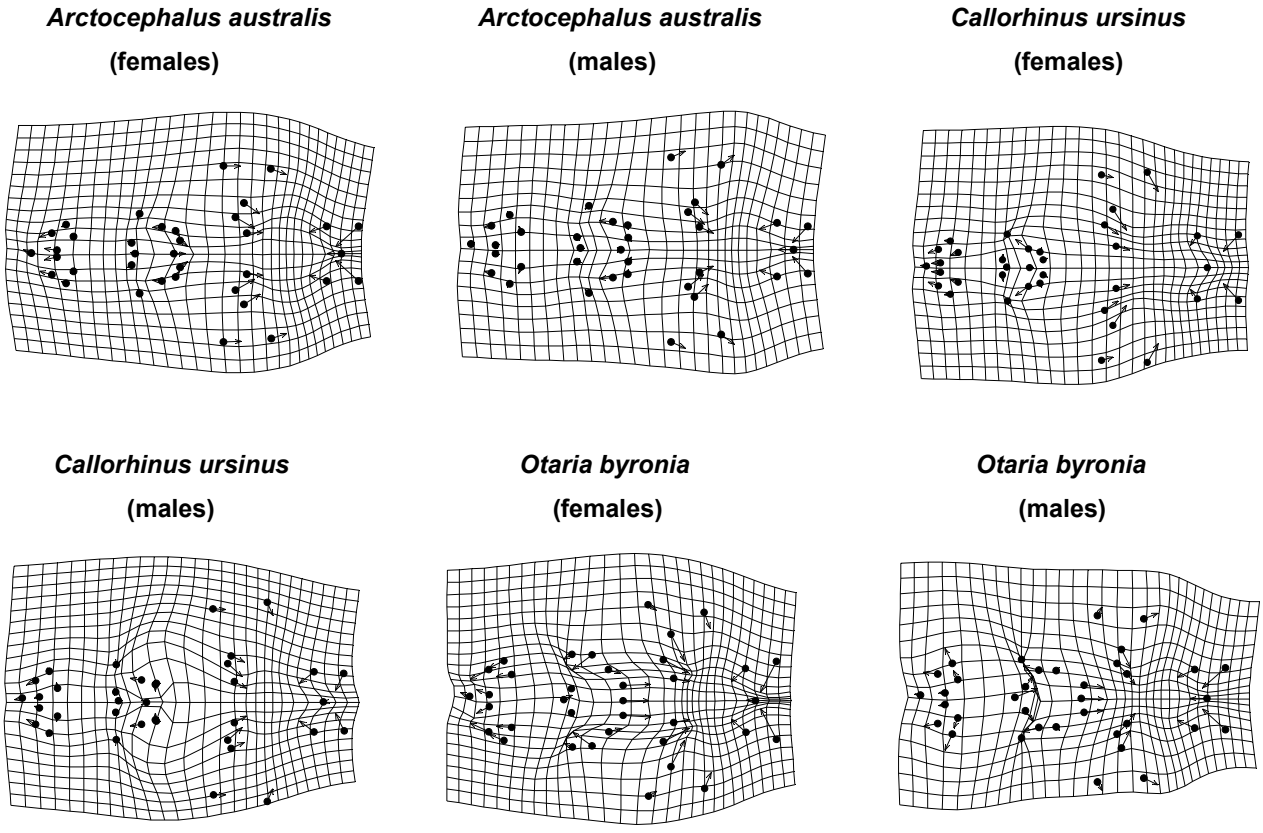


Figure 2. Ontogenetic transformations in shape. Each diagram depicts the regression of shape on

log-transformed centroid size as a Cartesian transformation using the thin-plate spline (BOOKSTEIN, 1996).

Lengths of Ontogenetic Trajectories –The ontogenetic trajectory of *C. ursinus* is the shorter and of *O. byronia* is the longer. A. *australis* has an intermediary length of ontogenetic trajectory. In the three species, the females have the longer trajectories, but the confidence intervals oflengths of trajectories overlap between the sexes of the same species. In the other hand, the lengths are significantly different between species (considering the sex pooling together or separately) (Table 4).

Table 4. Lenghts of ontogenetic trajectories in units of Procrustes distance. The confidence intervals are between parentheses.

Species	all specimens (95% CI)	females (95% CI)	males (95% CI)
A. australis	0.0099 (0.0084-0.0119)	0.0084 (0.0066-0.0106)	0.0062 (0.0052-0.0075)
C. ursinus	0.0053 (0.0040 – 0.00078)	0.0059 (0.0033-0.0081)	0.0038 (0.0020-0.0067)
O. byronia	0.0184 (0.0163-0.0217)	0.0162 (0.0131-0.0230)	0.0134 (0.0106-0.0167)

Shape disparity-For the sample comprising all three species disparity increases significantly over ontogeny once the disparity of the adults is near the double of the disparity between juveniles (Table 5). For any ontogenetical stage, *O. byronia* is the species that more contributes for the disparity of the all group, followed by *C. ursinus* (Table 5).

Groups	Juvenile disparity	95th Percentile of the within-species range	Subadult disparity	95th Percentile of the within-species range	Female adult disparity	95th Percentile of the within-species range	Male Adult disparity	95th Percentile of the within-species range
All species	0.00603	0.00540-0.00733	0.00983	0.00896-0.01131	0.00972	0.00885-0.01074	0.01128	0.01043-0.01247
	0.006	0.0056-0.0123	0.0089	0.0074-0.0108	0.0116	0.0102-0.0138	0.0123	0.0109-0.0145
A. australis	0.00266	0.00228 -0.00408	0.00210	0.00167-0.00324	0.00277	0.00175-0.00352	0.00124	0.00105-0.00179
x *C. ursinus*	0.0026	0.0016 to 0.0046	0.0015	0.0010-0.0032	0.0038	0.0028-0.0065	0.0022	0.0016 to 0.0037
A. australis	0.00497	0.00436-0.00712	0.01043	0.00953-0.01158	0.00963	0.00878-0.01075	0.01417	0.01268-0.01623
x *O. byronia*	0.056	0.0042-0.0112	0.0104	0.0094-0.0119	0.01	0.0081-0.0132	0.0134	0.0105-0.0167
***C. ursinus* x**	0.01047	0.00954-0.01253	0.01698	0.01465-0.01983	0.01729	0.01551-0.01989	0.01846	0.01688-0.02089
O. byronia	0.0099	0.0086-0.0156	0.0147	0.0113-0.0187	0.0210	0.0159-0.0261	0.0212	0.0184--0.0243

Table 5. Shape disparity, measured as the square root of the average of the squared distances between the mean shape of each species and the centroid, for the 3 species studied. Confidence intervals (CI) are obtained by resampling. In the first line it is presented the disparity without correction for size and in the second line it is presented the level of disparity with the correction of size using one different size for each subsample.

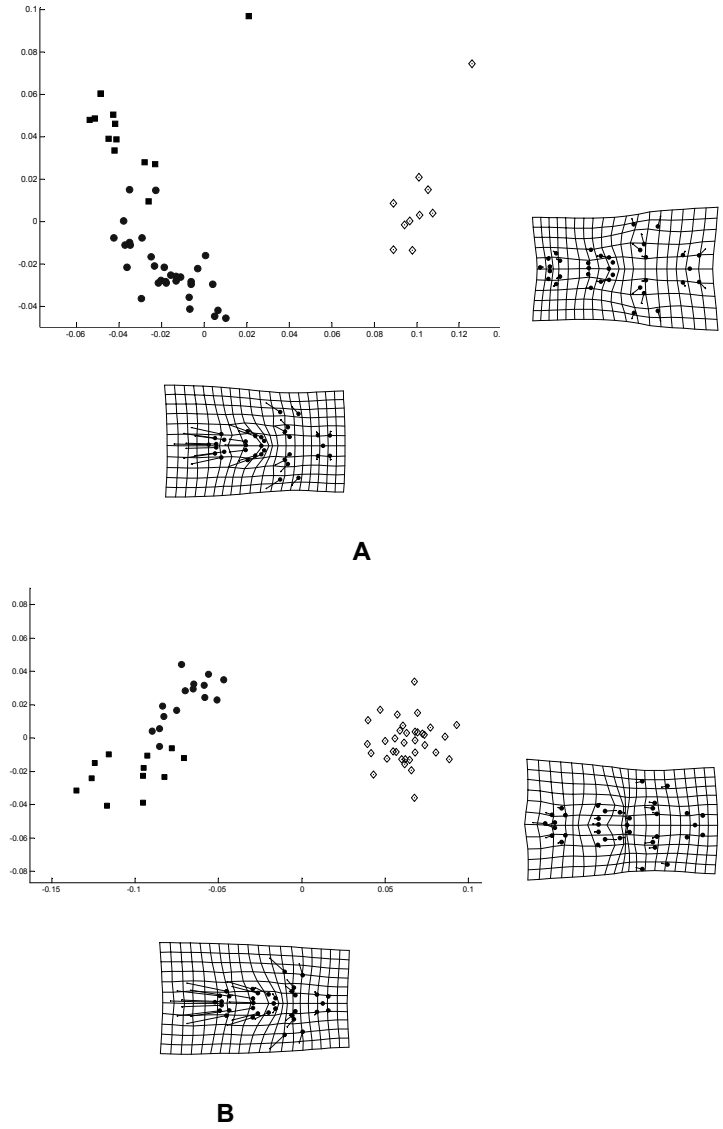
		Partial disparity	Standard Error	PD with size correction	Standard Error
JUVENILES	*Aa*	0.00053	0.00143	0.00072	0.00115
	Cu	0.00236	0.00136	0.00216	0.00123
	Ob	0.00314	0.00150	0.00314	0.00104
SUBADULTS	*Aa*	0.00089	0.00259	0.00101	0.00217
	Cu	0.00307	0.00246	0.00242	0.00231
	Ob	0.00587	0.00262	0.00544	0.00218
ADULT	*Aa*	0.00072	0.00256	0.00071	0.00325
FEMALES	*Cu*	0.00327	0.00271	0.00439	0.00263
	Ob	0.00574	0.00232	0.00648	0.00356
ADULT MALES	*Aa*	0.00136	0.00344	0.00108	0.00343
	Cu	0.00279	0.00274	0.00370	0.00327
	Ob	0.00713	0.00271	0.00747	0.00343

Table 6. Contributions to the disparity for each species, without and with size correction (*Aa*= *Arctocephalus australis*; *Cu*= *Callorhinus ursinus*; *Ob*=*Otaria byronia*)

Of course, when we compare the species in pairs, each species contributes equally to the shape disparity in all pairs of combinations between species. Comparing the two species of fur seals, the level of disparity is nearly static over the course of ontogeny, especially in the females (but with some increment when we analyze the disparity applying the size correction). In the males we observed a decrease (Table 6). Comparing *A. australis* with *O. byronia*, it was denoted that the level of disparity increases early in ontogeny, but after the subadult stages it nearly stabilizes. The disparity between *C. ursinus* and *O. byronia* is high and constant during all the development, with a not very conspicuous increment in the early ontogeny, but this level was almost two times higher in the adults of both sex when the size correction was performed. The disparity between the sea lion and the other two species is similar, considering the range of the confidence intervals (and when the size correction is not applied).

***Pattern of shape disparity*:** When we consider the three species together, the pattern of disparity do not modify a lot during ontogeny (Fig. 3). In the variance of the juvenile shape, two significant components were found: the first apart the fur seals species of the sea lion species (Fig. 3A). *O. byronia*, which presents high scores in that component, is differentiated from those with low scores by the greater extension of the palate (and by consequence, the shorter coanas), the deepening of the braincase and it in comparison with the rostrum. The second component describes the enlargement of the rostrum and the forward displacement of the coanes, but the more conspicuous pattern of changes in shape explained by this component is the postero-distalexpansion lateral and posterior of the braincase. *A. australis* has the lowest scores in that component and *C. ursinus* the highest. In the subadults, the first principal component is responsable by the enlargement of the rostrum and the mastoid process region and the second principal component express the enlargement of the posterior region of the bone palate.

In the adults, for both sexes, the enlargement in length and width is expressed largely for the PC1 (except in the condyle regioon), and the PC2 is related with changes in the posterior regions of the bone palate (females) or modifications in the posterior regions of the alveolar process (males).



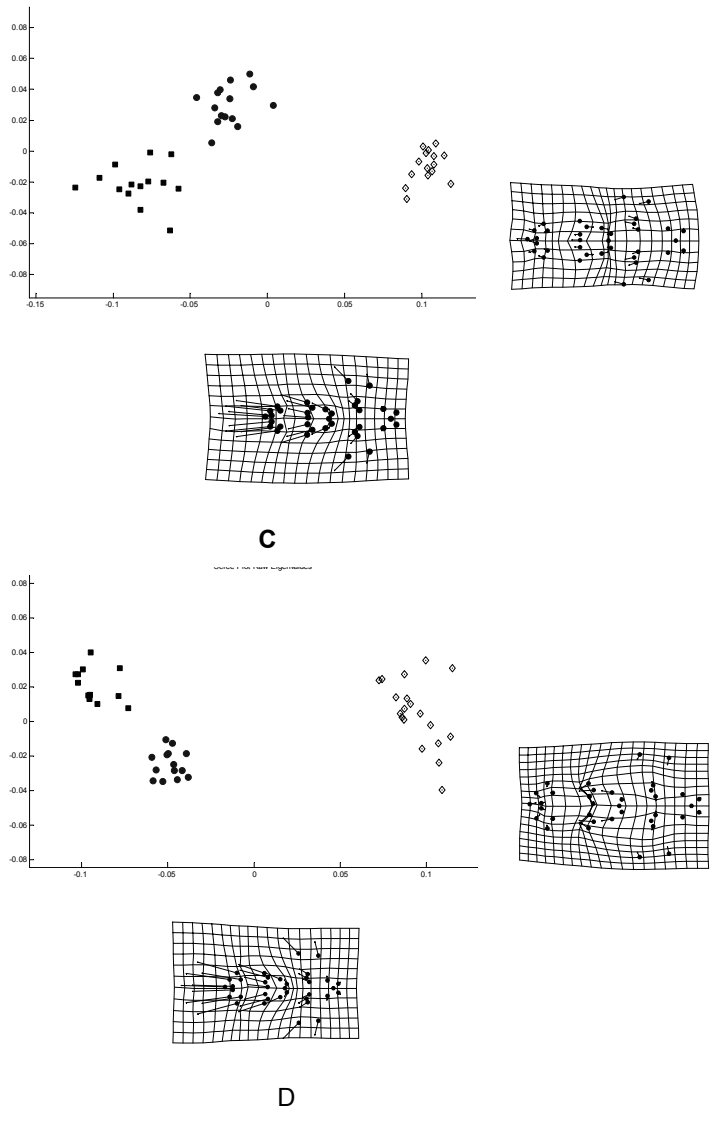


Fig. 3.Principal components analysis of shape pooling all species together. (A) juveniles shapes (PC1=0.4004, PC2= 0.2001); (B) subadult shapes (PC1=0.7281, PC2=0.0538); (C) adult females shapes (PC1=0.7479, PC2= 0.0662); (D) adult males shape (PC1=0.7350, PC2=0.0502). The difference between low and high scores on each axis is plotted as deformations using the thin-plate spline technique. Circles=*Arctocephalus australis*, Squares= *Callorhinus ursinus*, losangles= *Otaria byronia*

In this context, we can figure out that early ontogenies (allometric patterns) are similar and the initial stages overlap in shape space. In contrast, subadults is a confuse age group that sometimes disturb the clearness of the results with its heterogeneity and with its high variance. In fact, it is important to consider here that including the mean shape of the subadult females and males are very near the level of significance (p=0.055) in *O. byronia,* which surely increases the heterogeneity of this subgroup.

DISCUSSION

Ontogenies examined herein are clearly not constrained: nearly every developmental parameter of shape that can evolve does. The species are different in the initial and later shape of the skull, in the length of the ontogenetic trajectories and in the allometric pattern. So, we perceive a complex scenario where it is difficult to establish a relationship between the developmental processes with the phylogeny, overall because we had considered only 3 species. It is possible that if all species of the family were examined we would be more able to determine the causal relations between ontogeny and phylogeny in otarids. Thus, it will be very interesting to analyze what is exactly the relevance of evolution and development for the otarids history. The species do not conserve the same ontogenetic trajectory, so their evolution can not be explained only by a heterochronic hypothesis.

The stronger differences in the repatterning of the allometry occur in the later ontogeny, but *C. ursinus* and *O. byronia* are extremely different in all ontogeny. The result that the disparity is higher when all the species are pooled together is logical and attempted. Similarly, the high sea lion partial contribution to disparity is congruent with all the other results about the comparisons between shape in these species.

Concomitantly with the allometric repatterning, the lengths of the ontogenetic trajectories are different too, so complex changes are acting in the evolving ontogenies of these otarid species. However the impact of each evolutionary pattern to the disparity (counterbalance or amplification) it is difficult to design without modeling hypothetical ontogenies.

The hypothesis of amplification predicts that the interaction among several novelties enhances disparity above the level we would anticipate for their separate effects. And the hypothesis of counterbalancing predicts that the interaction among several novelties diminishes the impact of combined novelties. The most probable one, here, is the occurrence of amplifications once a time the ontogeny is not constrained and we had not found evidences of counter-balancing in the disparity, which revealed a trend to increase during ontogeny.

APENDIX 1. ANATOMICAL DESCRIPTION OF THE LANDMARKS

1- anteriormost point of the pré-maxilla tuberosity
2- antero-lateral extremity of third incisive alveolus
3- anteriormost point of incisive foramen
4- lateral extremity of canine alveolus
5- anteromedial point of first post-canine alveolus
6- anteriormost point of the maxilla-palatine suture
7- point that label the direction change of the maxilla-palatine suture
8- posteriormost point of the root at the lateral limit at bone palate of zigomatic process of the maxilla
9- posteriormost point of sixth post-canine alveolus
10- posteriormost point of palatine extension of maxilla (“pterygoid” process of the maxilla)
11- posteriormost point of interpalatine suture
12- point that label the direction change of the posterior border of palatine
13- posteriormost extremity of oval foramen
14- lateral extremity of jugal-esquamosal suture
15- medial extremity of the contact between the glenoid fossa and the ectotympanic
16- anteriormost extremity of the anterior aperture of carotid canal
17- antero-lateral corner of mastoid process
18- posteriormost point of the condiloid foramen
19- posteriormost point of occipital condyle
20- anteriormost point of foramen magnum.

3 CONCLUSÕES FINAIS

- Estudos ontogenéticos quantitativos são úteis para a avaliação e comparação de morfologias, constituem-se em um método muito mais robusto do que a comparação restrita à morfologia dos adultos e colaborando, inclusive, para a detecção de homoplasias. De fato, desde D´Arcy Thompson e Huxley (primeira metade do século XX) aos dias de hoje, novos e diferentes tratamentos foram dados à integração/correlação morfológica e ao estudo do desenvolvimento e tais avanços estão diretamente vinculados aos progressos nas áreas que tangem a interface ontogenia/evolução e a maturidade da biologia do desenvolvimento. Logicamente, descrições precisas da integração morfológica são cruciais, tanto para que se encontre uma explicação epigenética plausível para as trajetórias ontogenéticas, quanto para explorar com propriedade a relação entre o desenvolvimento e a evolução.

- As diferenças observadas entre as espécies atingem grandes magnitudes e indicam que uma complexa combinação de padrões de evolução atuou/atua sobre as morfogêneses e seus parâmetros-chave. Um estudo de modelagem das ontogenias (onde a labilidade de determinados parâmetros fosse manipulada em múltiplas combinações) poderia elucidar este intrigante quadro. Esta abordagem revelaria e elucidaria a atuação do "contra-balanceamento" (interações não-aditivas) ou das amplificações entre as novidades evolutivas no caso de estudo. Deste modo, o entendimento da relação da ontogenia do crânio com a rápida diversificação dos otarídeos recentes seguramente seria ampliado.

- Ontogenias não são meramente seqüências de eventos que ocorrem em uma determinada ordem temporal que pode ser retardada ou acelerada. São muitas as relações entre os eventos do desenvolvimento, e qualquer mudança em qualquer destes eventos (parâmetros) pode ou não se configurar na mola propulsora de uma cascata de efeitos em estágios posteriores.

- A idade absoluta relaciona-se com a idade sutural em todas as espécies, mas com índices de correlação diferentes. Além disto, a correlação não é linear. Dentro deste contexto, exemplares de *O. byronia* subadultos podem apresentar a sutura basal aberta, o que não ocorre em animais menores como *A. australis* e *C. ursinus*. Isto deve ser considerado ao estabelecer os métodos de determinação da maturidade física bem como ao se comparar fases ontogênicas de espécies diferentes, de modo que estas efetivamente correspondam a estágios biologicamente comparáveis.

- A maior similaridade entre os resultados das análises da ontogenia e da alometria, utilizando a morfometria geométrica e a morfometria dita tradicional, na espécie *Otaria byronia* pode ser um sinalizador da importância do tamanho amostral.

- O grau de diferença entre diversos aspectos das ontogenias das espécies aqui enfocadas aumenta de *C. ursinus* para *O. byronia*, em concordância com sua posição na hipótese das relações filogenéticas entre os gêneros desta família. - Os níveis de dimorfismo sexual são determinados pelo padrão alométrico (com exceção de *C. ursinus*) e possivelmente também pelo tamanho da trajetória, ainda que a significância desta não tenha sido demonstrada.

- O parâmetro tamanho da trajetória revelou-se proporcional ao tempo de desenvolvimento e crescimento nos grupos estudados.

- Modificações na taxa do desenvolvimento morfológico com relação ao tempo foram demonstradas através das diferenças nas inclinações das linhas de regressão entre os grupos comparados, mas isto não se qualifica como um resultado heterocrônico, uma vez que as trajetórias ontogenéticas não são comparáveis. Outrossim, é mister lembrar que o tamanho foi uilizado como variável independente. Sendo

assim, faz-se necessário uma continuação deste estudo com uma ampliação da amostra e da determinação das idades absolutas para que esta problemática possa ser resolvida.

Machos e fêmeas de *A. australis* não diferiram na constante de crescimento ou desenvolvimento nem tampouco quanto à inclinação dos modelos lineares empregados para descrever as respectivas trajetórias quando a co-variável empregada foi a idade absoluta. Entretanto, ao se utilizar o tamanho, como variável os sexos revelaram pendentes significantemente distintas.

Ao se analisar a covariância entre mudança da forma e a idade absoluta, machos e fêmeas de *C. ursinus* diferiram na taxa de crescimento mas não na taxa de desenvolvimento. Todavia, os resultados da covariância entre a morfogênese e o tamanho revelaram que machos e fêmeas desta espécie diferem com respeito à constante (o qual pode ser interpretado como ponto inicial da trajetória ontogenética, neste caso).

Apenas *O. byronia* apresentou dimorfismo sexual quanto à alometria avaliada através da análise multivariada das medidas lineares (mas aqui o vetor alométrico não foi perfeitamente isolado dos componentes de forma).

- É preciso cautela nas conclusões embasadas nas relações aqui apresentadas, pois há grandes diferenças nos tamanhos amostrais, sobretudo entre *Callorhinus ursinus* e *Otaria byronia.* Além disto, também é preciso ter em conta que uma única vista craniana foi analisada através da morfometria geométrica.

- As análises tradicionais são limitadas pela premissa de que as distâncias são homológas entre os taxa analisados, mesmo quando as distâncias estejam refletindo a evolução das próprias estruturas. Uma outra limitação é a redundância parcial da informação sobre a forma, que enfraquece o poder dos testes estatísticos para detectar as diferenças morfológicas. Em contrapartida, métodos geométricos descrevem a forma preservando a posição relativa dentre os marcos anatômicos.

- No momento em que a morfometria geométrica define e captura a informação relacionada ao tamanho mais efetiva e claramente, permite, por conseguinte, a correta remoção dos efeitos de escala de toda a configuração de marcos anatômicos de modo mais eficiente do que qualquer outro protocolo empregado em técnicas de morfometria tradicional. Esta questão é mister, uma vez que se há confusão da forma com o tamanho onde a prejudica a análise da alometria está irremediavelmente prejudicada, assim bem como o papel da alometria como um fator limitante para as mudanças evolutivas.

-A morfometria tradicional está limitada também pelo fato de fornecer informações apenas no que se refere a diferenças entre os grupos que estão alinhados naquele eixo. Já as coordenadas retangulares, associadas com os marcos anatômicos, capturam a variação em todas as direções possíveis no espaço da figura sem gerar problemas que concernem à dimensionalidade[47].

- A heterocronia dissociada chegou a ser considerada uma regra (FINK 1982; McNAMARA 1988; REILLY et al. 1997) na evolução do desenvolvimento, uma vez que heterocronias dissociadas podem ser inferidas à toda e qualquer característica que não tenha evoluído segundo o modelo da heterocronia global. Entretanto, modularidade no sistema ontogenético apenas é uma hipótese explicativa razoável quando as variáveis individuais corresponderem a partes ou processos individuais e dissociáveis no desenvolvimento um dos outros, o que não parece ser o caso do crânio dos mamíferos (ZELDITCH et al. 1992). Ora, a morfogênese é, sabidamente, epigenética e estudos evolutivos que se restringem a analisar características

[47] E devemos recordar que a dimensionalidade de um conjunto de dados é muito importante para que a determinação do tamanho amostral minimamente adequado, de tal sorte que a morfometria geométrica permite a maximização das amostras.

isoladas da morfologia craniana ou que comparam a ontogenia de partes individuais do crânio, configuram-se, implicitamente como pré-formacionistas no que concerne ao desenvolvimento. Outrossim, o desconhecimento acerca da integração no desenvolvimento do crânio compromete estudos comparativos inter-específicos das ontogenias deste crânios, bem como do adequado entendimento da expressão de fenômenos como o dimorfismo sexual, tardiamente expresso nas espécies aqui avaliadas.

- Em estudos futuros, recomenda-se avaliar a variância das mudanças na forma em cada idade de modo a poder determinar o quanto da variação da forma é explicado pelo efeito do tamanho e o quanto é função do tempo de desenvolvimento. Esta análise não foi possível no presente trabalho uma vez que a determinação da idade foi feita em anos, sendo, por conseguinte, pouco específica para este fim (ao longo de um ano, podem ser confundidas a variabilidade com as mudanças relacionadas à própria ontogenia no decorrer deste tempo).

- Em meio a tantas novas abordagens e efervescentes controvérsias, não é justificável que uma minoria julgue deter todas as soluções e denegrir outros tratamentos no que se refere à forma. Com efeito, indubitavelmente, forma e padrão são assuntos plenos de informações, avanços e surpresas. Logo, não há uma única solução correta (ou melhor), e muitas das metodologias mais recentemente desenvolvidas são ainda razoavelmente pouco familiares à maioria dos investigadores envolvidos/interessados.

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