UNIVERSIDADE FEDERAL DO PARANÁ

RITA MELO FRANCO SANTOS

COMPARATIVE DESCRIPTION OF THE BEAKS OF *Chiroteuthis* (*cf*) *veranyi* FÉRUSSAC, 1835, *Liocranchia reinhardti* STEENSTRUP, 1856, AND *Doryteuthis opalescens* BERRY, 1911 PARALARVAE (CEPHALOPODA: TEUTHOIDEA)

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Orientadora: Prof.ª Dr.ª Érica Alves González Vidal

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POR

Rita Melo Franco Santos

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“A cura para tudo é sempre água salgada:
o suor, as lágrimas ou o mar.”

Isak Dinesen

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Um enorme obrigada e um sorriso generoso

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“O universo ajuda-nos sempre a lutar pelos nossos sonhos, por mais idiotas que possam parecer. Porque são os nossos sonhos, e só nós sabemos o quanto nos custa sonhá-los.” (Paulo Coelho)

SUMÁRIO

RESUMO

Estudos sobre o desenvolvimento morfológico do bico nos estágios iniciais do ciclo de vida de um cefalópode podem aumentar o conhecimento sobre a ecologia de paralarvas, mas são raros na literatura. No presente trabalho foram examinados bicos de 18, 16 e 31 paralarvas de *Chiroteuthis* cf. *veranyi* (3,62 a 13,62 mm comprimento do manto (CM)), *Liocranchia reinhardti* (2,80 a 20,63 mm CM) e *Doryteuthis opalescens* (2,25 a 12,30 mm CM), respectivamente. As estruturas das mandíbulas superior (MS) e inferior (MI) foram medidas e os valores foram comparados ao CM por regressão linear múltipla, de forma a determinar as influências relativas de cada uma no crescimento. Cada estrutura foi comparada entre espécies através de ANOVA para detectar possíveis diferenças. As mandíbulas apresentaram diferentes níveis de desenvolvimento e mudanças marcadas puderam ser observadas em CM distintos. Coloração foi observada principalmente em *L. reinhardti* e em *D. opalescens*. As paredes laterais e capuz (MS) e asas e paredes laterais (MI) foram as estruturas mais robustas, com uma importância significativa também do rostro (MI) para *L. reinhardti*. Dentes (MI) e uma fenda no rostro, características de cefalópodes ancestrais, foram observados em todas as espécies. Essas estruturas desapareceram total e parcialmente (fenda persistente) nos maiores indivíduos de *L. reinhardti* e *D. opalescens*, respectivamente, e foram retidas em todos os indivíduos analisados de *C.* cf. *veranyi*. Os resultados deste estudo revelam informações importantes sobre a morfologia funcional do bico durante os primeiros estágios do ciclo de vida de um cefalópode.

Palavras-chave: bico, cefalópode, *Chiroteuthis*, *Doryteuthis*, *Liocranchia*, paralarva.

ABSTRACT

Studies on the early morphological development of cephalopod beaks can improve knowledge on paralarval ecology, but are rare in the literature. Beaks of 18, 16, and 31 paralarvae of *Chiroteuthis* cf. *veranyi* (3.62 - 13.62 mm mantle length (ML)), *Liocranchia reinhardti* (2.80 - 20.63 mm ML), and *Doryteuthis opalescens* (2.25 - 12.30 mm ML), respectively, were examined. Measurements were taken from structures of upper (UJ) and lower (LJ) jaws, and values were compared against ML by multiple linear regression to determine relative influences on growth. Structures were compared by ANOVA to identify specific differences. The UJ and LJ showed different development and morphological changes occurred at distinct MLs. Coloration was observed mostly in *L. reinhardti* and *D. opalescens*. Lateral walls and hood (UJ) and wings and lateral walls (LJ) were the most robust structures, together with the rostrum (LJ) for *L. reinhardti*. Teeth (LJ) and slit, characteristics of ancestral cephalopods, were observed, disappearing completely and partially (uncollapsed slit) on the largest specimens of *L. reinhardti* and *D. opalescens*, respectively, and remaining in all sizes of *C.* cf. *veranyi*. The results of this study reveal important information on the beak's functional morphology during the first stages of these species' life cycle.

Key words: beak, cephalopod, *Chiroteuthis*, *Doryteuthis*, *Liocranchia*, paralarvae

PREFÁCIO

A presente dissertação foi estruturada de forma que a primeira parte do trabalho, redigida em português, é composta por introdução, objetivos, hipótese, materiais e métodos e referências bibliográficas, enquanto a segunda parte, redigida em inglês e estruturada conforme as orientações da revista Hydrobiologia, inclui o artigo científico resultante da pesquisa de Mestrado, com introdução, materiais e métodos, resultados, discussão, conclusões e referências bibliográficas.

INTRODUÇÃO

Poucos são os estudos existentes sobre paralarvas da maioria de espécies de cefalópodes (Boyle, 1990) e pouco se sabe sobre suas histórias de vida no período pós-eclosão (Zeidberg & Hamner, 2002).

Chiroteutídeos são cefalópodes gelatinosos e amoniacais que possuem longos braços ventrais (Clarke, 1986), e cuja distribuição inclui águas circumglobais (Jereb & Roper, 2010) meso e batipelágicas, com exceção das altas latitudes (Roper & Sweeney, 1992). A família possui uma característica única, um estágio paralarval de duração desconhecida chamado *Doratopsis*, o qual é completamente diferente de qualquer outra fase do ciclo de vida de um cefalópode (Young, 1991). Durante seu desenvolvimento, paralarvas de *Chiroteuthis veranyi* (Figura 1a) sofrem mudanças morfológicas marcantes, as quais não são completamente conhecidas. As paralarvas podem ser encontradas nas primeiras centenas de metros de profundidade (Young & Roper, 1998), entre 200 a 300 m (Jereb & Roper, 2010) até 600 m (Roper & Young, 1975), aonde chegam a atingir grandes tamanhos (CM de até 90 mm, Young & Roper, 1998), mas após o estágio *Doratopsis* ocorre uma migração ontogenética, não muito bem definida, para águas bati ou meso-batipelágicas, isto é, 2000 a 3000 m de profundidade (Young & Roper, 1998; Jereb & Roper, 2010).

Os cranchídeos, lulas pelágicas e semi-pelágicas, possuem um manto no formato de uma grande câmara de flutuação (Roper et al., 1984), o que os torna organismos lentos; seu porte varia de pequeno a gigante (Nesis, 1999). São cosmopolitas e ocorrem em grandes quantidades em águas oceânicas desde o Subártico até a Antártica, sendo encontrados entre a superfície e profundidades maiores que 2000 m. A história de vida dos cranchídeos indica que o crescimento em estágios iniciais ocorre em águas superficiais, sendo seguido por uma migração ontogenética para maiores profundidades, onde ocorre a maturação (Voss et al., 1992). *Liocranchia reinhardti* é uma espécie de rápido crescimento, com um ciclo de vida caracterizado por duas fases relacionadas à profundidade em que se encontra o indivíduo (Arkhipkin, 1996). Na primeira fase as paralarvas (Figura 1b), juvenis e subadultos podem ser encontrados em águas epi e mesopelágicas, entre 0 e 500 m de profundidade (Nesis, 1987), onde se alimentam e atingem entre 170 e 200 mm CM em 4 a 5 meses. Paralarvas de pequeno tamanho provavelmente ascendem para águas epipelágicas após a eclosão, como verificado em águas oceânicas superficiais do Atlântico Norte, onde foram capturados indivíduos de 2,4 mm CM (Arkhipkin et al., 1988). A segunda fase é caracterizada pela migração para águas mais profundas, onde ocorre a maturação e a desova subsequente (Nesis, 1987; Arkhipkin, 1996).

Loliginídeos podem ser encontrados em todo o mundo, com exceção das regiões polares, mas estão geralmente limitados às águas neríticas anteriores à quebra da plataforma continental. *Doryteuthis opalescens* (Figura 1c), a qual pode ser encontrada desde a superfície até 500 m de profundidade nas primeiras 200 milhas da costa, é endêmica à Corrente da Califórnia, ocorrendo entre a porção mais ao sul do México (Península da Baixa Califórnia, 22^o N) e o sudeste do Alasca (58^o N) (Jereb & Roper, 2010). Os indivíduos vivem pouco tempo, cerca de 9 a 10 meses (Jackson, 1994), e podem atingir a maturidade a partir de 6 meses (Butler et al., 1999). Os tamanhos são geralmente pequenos a medianos, em média 140 a 170 mm CM (Jereb & Roper, 2010). Koslow & Allen (2011) observaram que a abundância de paralarvas em águas subsuperficiais foi maior à noite que durante o dia, indicando uma migração para o nêuston no período da noite.

O tema da diversificação de modos de desenvolvimento e da história evolutiva das paralarvas tem recebido pouca atenção no grupo dos cefalópodes, mas ambos são de grande importância na compreensão de diversos processos biológicos. *C. veranyi* e *L. reinhardti* são espécies chave na compreensão da história evolutiva de paralarvas, uma vez que as mudanças morfológicas pelas quais estas passam entre as fases de paralarva e juvenil/adulto são o que há de mais próximo a uma metamorfose para cefalópodes. Mudanças morfológicas durante a ontogenia não são tão pronunciadas em *D. opalescens*.

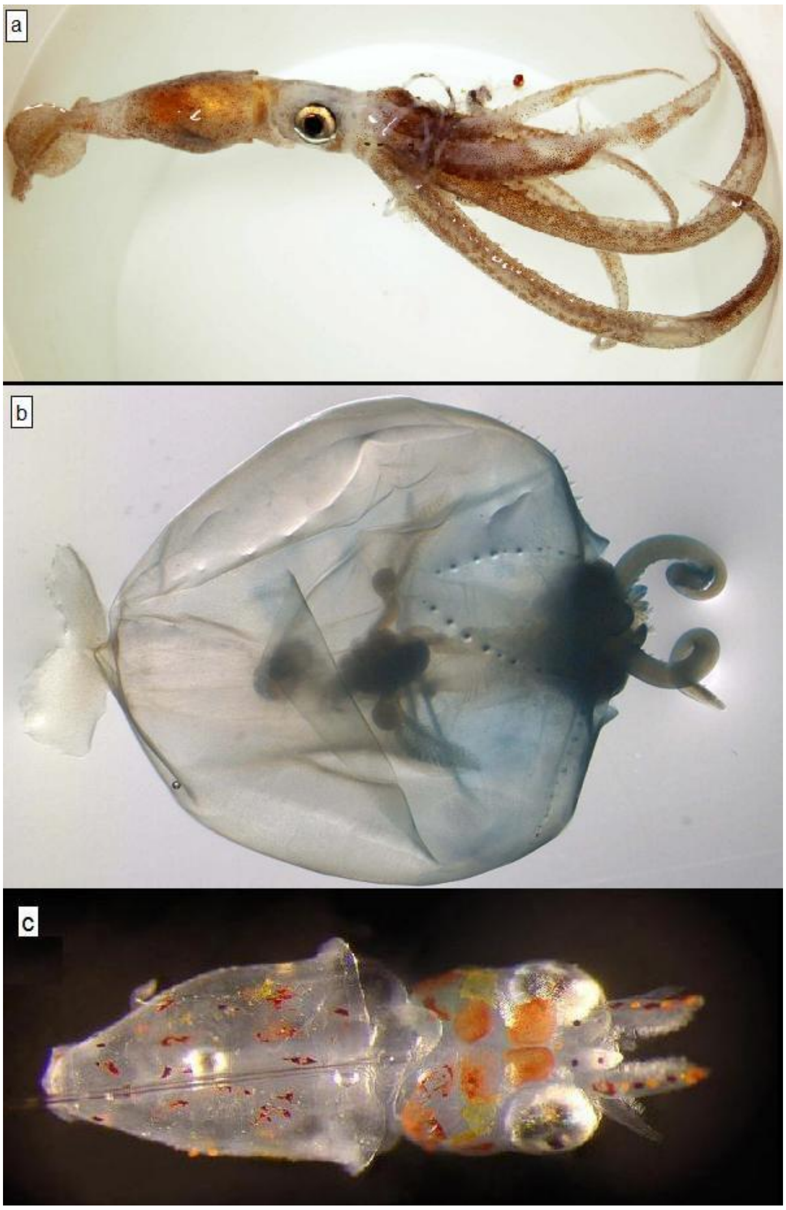

Figura 1: Paralarvas das espécies investigadas no presente estudo: (1a) *Chiroteuthis veranyi*; (1b) *Liocranchia reinhardti*; (1c) *Doryteuthis opalescens*.

Fontes: (1a) http://cientistapolarjxavier.blogspot.com/2009/04/boa-pascoa-happy-easter.html; (1b) a autora; (1c) http://calphotos.berkeley.edu/browse_imgs/cephalopod_sci_1.html.

Estudos sobre as estruturas bucais de paralarvas de cefalópodes e seu desenvolvimento ontogenético são raros na literatura, mas fundamentais para compreender melhor sua ecologia. O bico, uma estrutura quitinosa encontrada na massa bucal, é uma poderosa ferramenta de alimentação, a qual, associada a uma potente musculatura, é utilizada para dilacerar pequenos pedaços das presas. Ele é composto pelas mandíbulas superior (MS) e inferior (MI), as quais diferem entre si tanto em morfologia quanto em função (Raya & Hernández-González, 1998). Devido à sua importância direta na alimentação e no desenvolvimento, o bico (e suas características) de espécies oceânicas cuja ontogenia inclui mudanças morfológicas marcantes, tais como *C. veranyi* e *L. reinhardti*, pode ser contrastado com aquele de espécies costeiras, como *D. opalescens*. Tal comparação poderia, possivelmente, apresentar oportunidades para o teste de hipóteses sobre a diversificação de modos de desenvolvimento e sobre a evolução de paralarvas de cefalópodes. Dessa forma, o objetivo deste estudo foi examinar a morfologia e morfometria das estruturas bucais das paralarvas de *C.* cf. *veranyi*, *L. reinhardti* e *D. opalescens* durante os estágios iniciais do ciclo de vida e comparar as estruturas mais importantes entre as espécies. Essa informação pode apresentar novas perspectivas sobre os distintos modos de desenvolvimento de espécies oceânicas e neríticas.

OBJETIVOS

Descrever a morfologia e a morfometria dos bicos de paralarvas de *Chiroteuthis* cf. *veranyi* (Chiroteuthidae), *Liocranchia reinhardti* (Cranchiidae) e *Doryteuthis opalescens* (Loliginidae), comparando as estruturas de suas mandíbulas, e verificar morfologica e morfometricamente se as duas primeiras espécies são semelhantes entre si, por serem oceânicas, e se ambas são diferentes da terceira, por esta ocupar o ambiente costeiro.

Objetivos Específicos

- Descrever a morfologia geral, coloração, formato e presença/ausência de dentes nas mandíbulas superior e inferior dos bicos de *C.* cf. *veranyi*, *L. reinhardti* e *D. opalescens*;
- Comparar os bicos das espécies avaliadas quanto à sua morfologia e função, determinando quais são semelhantes e/ou diferentes entre si.

HIPÓTESE

Se a estrutura do bico das paralarvas, definida a partir de dados de morfologia e morfometria, está relacionada ao ambiente no qual os indivíduos estão inseridos (oceânico, para *Chiroteuthis* cf. *veranyi* e *Liocranchia reinhardti*; e costeiro, para *Doryteuthis opalescens*), então as alterações no bico ao longo da ontogenia deverão ser semelhantes entre as espécies *C.* cf. *veranyi* e *L. reinhardti* e diferentes entre as duas e *D. opalescens*.

MATERIAIS E MÉTODOS

Paralarvas de *Chiroteuthis* cf. *veranyi* de 3,62 a 13,62 mm de comprimento de manto (CM) e de *Liocranchia reinhardti* de 2,8 a 20,63 mm CM foram amostradas a partir de arrastos de plâncton realizados durante diversos cruzeiros entre 1984 e 1997 na costa sul do Brasil (28^{o}30'S - 34^{o}40'S), utilizando-se redes Bongo de 60 cm de diâmetro e malha de 300 µm. Arrastos oblíquos foram realizados entre a superfície e aproximadamente 300 m de profundidade. Após serem coletadas, as paralarvas foram fixadas em formol a 4%.

Paralarvas de *Doryteuthis opalescens* de 2,25 a 12,30 mm CM foram cultivadas no Centro Nacional de Recursos para Cefalópodes (NRCC) da University of Texas Medical Branch em Galveston, Texas (EUA) pela Dr^{a} Érica Vidal entre 1997 e 2000. Os ovos foram coletados em áreas de desova na costa da Califórnia e levados para o laboratório, onde foram cultivados a 16 ± 1^{o}C durante 1 a 70 dias após a eclosão e alimentados com uma mistura de náuplios enriquecidos de *Artemia*, copépodes (em diversos estágios de desenvolvimento) e misidáceos (*Americamysis almyra*) (Vidal et al., 2002a). A metodologia detalhada pode ser encontrada em Vidal et al. (2002a, 2002b, 2006). Todas as paralarvas foram fixadas e preservadas em formol a 4% neutralizado.

A extração e armazenamento dos bicos de 18, 16 e 31 paralarvas de *C.* cf. *veranyi*, *L. reinhardti* e *D. opalescens*, respectivamente, foram realizados de acordo com a metodologia descrita em Franco-Santos (submitted).

A massa bucal foi obtida descartando-se a região do manto das paralarvas e expondo a cabeça a uma solução de 30% hipoclorito de sódio e 70% de água destilada, capaz de dissolver a musculatura, permitindo a extração do bico. Foi necessário um cuidado especial nesta etapa, uma vez que o hipoclorito de sódio pode alterar a pigmentação dos bicos, além de deixá-los frágeis e suscetíveis à quebra. Dissolvida a musculatura, os bicos foram imersos em água destilada em uma lâmina escavada para a obtenção de imagens digitais, e manuseados com micropinças, de forma a não danificá-los. Após a obtenção de imagens os bicos foram armazenados em álcool a 70%, de acordo com a recomendação de Clarke (1986).

Imagens digitais das mandíbulas superior (MS) e inferior (MI) foram obtidas com uma câmera Olympus modelo SC20-GA acoplada a um microscópio estereoscópico Olympus modelo SZX7. A captação das imagens teve orientação ventral e dorsal para a MI e MS, respectivamente, e as medidas foram adquiridas por meio de projeção de retas sobre essas imagens pelo software livre Image J (Rasband, 1997) (versão 1.46).

A descrição morfológica das mandíbulas foi feita através de observações visuais durante e após a captura de imagens. As descrições foram feitas para intervalos de tamanhos (CM), i.e. uma (ou ambas) mandíbula de um indivíduo de determinado tamanho só foi descrita caso apresentasse diferenças em relação àquela do último tamanho descrito. As mensurações de estruturas (Fig. 2) foram baseadas em Franco-Santos (submitted), retirando-se aquela do comprimento da base (CBS), excluída devido ao tamanho idêntico ao do comprimento da crista (CCR), e adicionando-se uma nova estrutura, a largura da mandíbula inferior (LMI).

Medidas da MS (Fig. 2a): comprimento do capuz (CC): reta que une o ápice do rostro na região anterior da mandíbula ao ponto apical do capuz em sua região aboral; comprimento do rostro (CR): reta que une o ápice do rostro a um ponto na reta da amplitude da mandíbula (AM), de modo que seja formado um ângulo de 90^o; amplitude da mandíbula (AM): reta que une os pontos onde se inicia a protrusão do rostro; abertura da parede lateral (APL): reta que une os pontos mais extremos (região anterior) da base das paredes laterais; comprimento da mandíbula superior (CMS): reta que une o ponto extremo da região posterior da mandíbula superior ao ponto que forma um ângulo de 90^o com a reta da APL; largura da mandíbula superior (LMS): reta que une os pontos mais extremos da parede lateral quando se visualiza a região dorsal da mandíbula superior.

Medidas da MI (Fig. 2b): comprimento do capuz (CC): reta que une o ápice do rostro ao ponto mais extremo do capuz na região posterior do bico; comprimento do rostro (CR): reta que une o ápice do rostro ao ponto que forma um ângulo de 90^o com a linha que define a amplitude da mandíbula (AM); amplitude da mandíbula (AM): reta que une os pontos onde se inicia a protrusão do rostro ou onde começa a dentição (caso ela exista); abertura da asa (AA): reta que une os pontos na base das asas, onde estas se elevam para formação do rostro; comprimento da asa (CA): reta que une o ponto mais extremo da asa, na região anterior da mandíbula, ao ponto em que esta se encontra com a parede lateral e inicia a elevação para a região do capuz; largura da asa (LA): reta que une os pontos laterais mais extremos da asa, desde o ponto onde termina a reta da AA até o ponto que limita a região externa da asa; comprimento da crista (CCR): reta que une o ponto onde se inicia o rostro (ou onde começa a dentição) ao ponto mais externo na crista (região posterior do bico); largura da mandíbula inferior (LMI): reta que une os pontos mais extremos da parede lateral quando se visualiza a região ventral da mandíbula inferior.

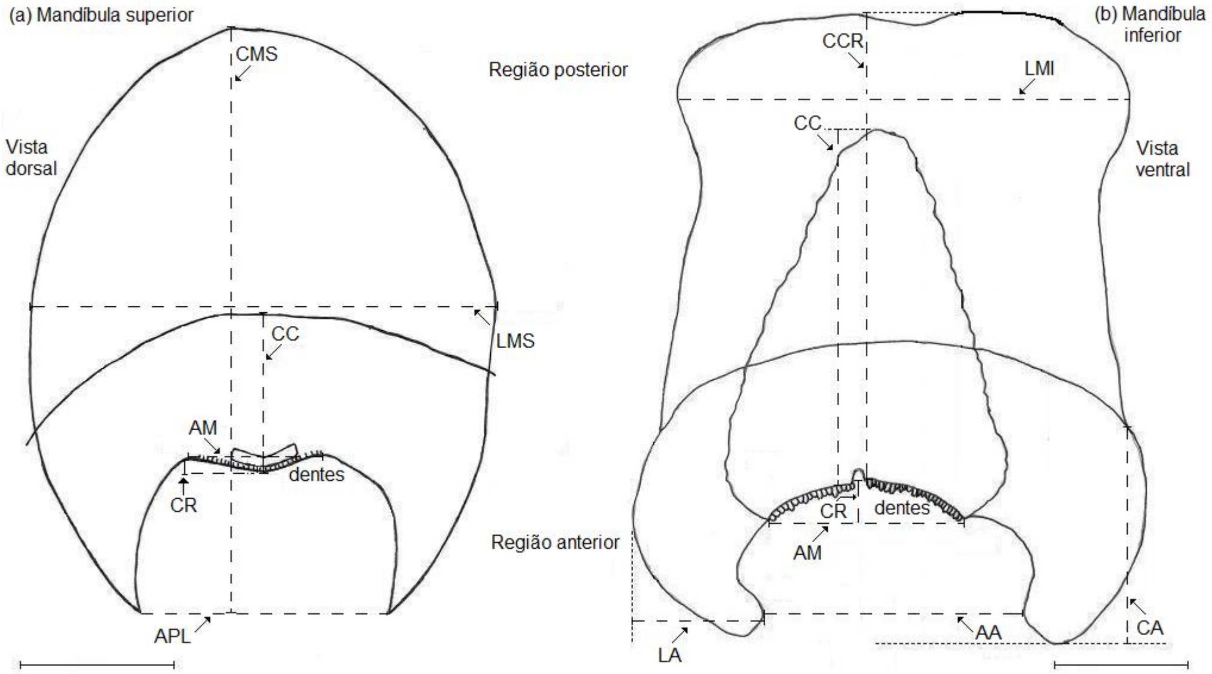

Figura 2: Desenho esquemático das mandíbulas superior (MS) e inferior (MI). (a) MS: CC = comprimento do capuz; CR = comprimento do rostro; AM = amplitude da mandíbula; APL = abertura da parede lateral; CMS = comprimento da mandíbula superior; LMS = largura da mandíbula superior. (b) MI: CC = comprimento do capuz; CR = comprimento do rostro; AM = amplitude da mandíbula; AA = abertura da asa; CA = comprimento da asa; LA = largura da asa; CCR = comprimento da crista; LMI = largura da mandíbula inferior. Os dentes são indicados em ambos (a) e (b). Escala = 100µm

Os bicos, além de serem medidos, foram caracterizados quanto ao formato, tamanho, padrão de coloração (resultado do escurecimento causado pela quinona às proteínas associadas com as camadas de quitina do bico), estrutura e presença/ausência de dentes, e a morfologia e morfometria destes foi comparada entre as espécies. O desenvolvimento da coroa de braços também foi analisado para as espécies, tendo sido observadas as características gerais, principalmente a fórmula de braços, o número de ventosas por braço e seu diâmetro e o comprimento do tentáculo. Indivíduos de diversos tamanhos de *C.* cf. *veranyi* e de *D. opalescens* foram analisados e o desenvolvimento da coroa de braços nessas espécies foi feita de acordo com classes de tamanho, enquanto que para *L. reinhardti* apenas um indivíduo (10,88 mm CM) foi analisado.

A relação entre as estruturas do bico e o crescimento do indivíduo foi analisada pelo modelo $\ln(Y) = \ln(a) + b_1 * \ln(X_1) + b_2 * \ln(X_2) + b_n * \ln(X_n) + e$, no qual a variável dependente é o CM, os parâmetros da regressão são os coeficientes de crescimento de cada estrutura do bico e as variáveis independentes são as estruturas do bico. O modelo foi reduzido manualmente através de regressão múltipla linear ‘stepwise’, de forma que foram determinadas as estruturas com maior influência (i.e., maior poder de explicação) no crescimento, assim como as equações de regressão linear múltipla, coeficientes de determinação múltipla (R^2) e valores para F e *P*. Os valores obtidos para as estruturas foram comparados entre as espécies através de ANOVA para determinar possíveis diferenças entre as mesmas. Alguns dos valores obtidos para o CR foram negativos e, nesse caso, foram transformados: houve substituição pela média do grupo (CR) para a determinada espécie quando os valores negativos eram < 30% do total de valores obtidos; e substituição por 0.1 quando os valores negativos perfaziam > 30% do total de valores obtidos. As análises estatísticas foram realizadas através do software livre R (Ihaka & Gentleman, 1993) versão 2.13.0.

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CAPÍTULO I

Comparative description of the beaks of *Chiroteuthis* (*cf*) *veranyi* Férussac, 1835, L*iocranchia reinhardti* Steenstrup, 1856, and *Doryteuthis opalescens* Berry, 1911 paralarvae (Cephalopoda: Teuthoidea)

Descrição comparativa dos bicos de paralarvas de *Chiroteuthis* (*cf*) *veranyi* Férussac, 1835, *Liocranchia reinhardti* Steenstrup, 1856 e *Doryteuthis opalescens* Berry, 1911 (Cephalopoda: Teuthoidea)

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Abstract

Studies on the early morphological development of cephalopod beaks can improve knowledge on paralarval ecology, but are rare in the literature. Beaks of 18, 16, and 31 paralarvae of *Chiroteuthis* cf. *veranyi* (3.62 - 13.62 mm mantle length (ML)), *Liocranchia reinhardti* (2.80 - 20.63 mm ML), and *Doryteuthis opalescens* (2.25 - 12.30 mm ML), respectively, were examined. Measurements were taken from structures of upper (UJ) and lower (LJ) jaws, and values were compared against ML by multiple linear regression to determine relative influences on growth. Structures were compared by ANOVA to identify specific differences. The UJ and LJ showed different development and morphological changes occurred at distinct MLs. Coloration was observed mostly in *L. reinhardti* and *D. opalescens*. Lateral walls and hood (UJ) and wings and lateral walls (LJ) were the most robust structures, together with the rostrum (LJ) for *L. reinhardti*. Teeth (LJ) and slit, characteristics of ancestral cephalopods, were observed, disappearing completely and partially (uncollapsed slit) on the largest specimens of *L. reinhardti* and *D. opalescens*, respectively, and remaining in all sizes of *C.* cf. *veranyi*. The results of this study reveal important information on the beak’s functional morphology during the first stages of these species’ life cycle.

Key words: beak, cephalopod, *Chiroteuthis*, *Doryteuthis*, *Liocranchia*, paralarvae

Introduction

Cephalopod paralarvae of most species are understudied and poorly understood (Boyle, 1990), and little is known on their early life history in the sea (Zeidberg & Hamner, 2002).

Chiroteuthids are gelatinous, ammoniacal squids which possess long ventral arms when compared to body size (Clarke, 1986), and whose distribution includes circumglobal (Jereb & Roper, 2010) meso to bathypelagic waters, except in high latitudes (Roper & Sweeney, 1992). They show a unique characteristic, a paralarval stage of unknown duration named *Doratopsis*, which is completely different than any other phase of the life cycle of a cephalopod (Young, 1991). *Chiroteuthis veranyi* Férussac, 1835 paralarvae undergo marked morphological changes, which are not fully known. Paralarvae are found in the upper few hundred meters (Young & Roper, 1998), from 200 to 300 m (Jereb & Roper, 2010) down to 600 m (Roper & Young, 1975), where they can attain large sizes (up to 90 mm ML, Young & Roper, 1998), but after the *Doratopsis* stage there is a poorly defined ontogenetic migration to bathy or meso-bathypelagic waters (2000 to 3000 m) (Young & Roper, 1998; Jereb & Roper, 2010).

The Cranchiidae, pelagic and semi-pelagic squids, have a mantle in the shape of a big flotation chamber (Roper et al., 1984), which makes them small to gigantic slow moving squids (Nesis, 1999). They are cosmopolitans and occur in large numbers in oceanic waters from the Subarctic to the Antarctic, being found between the surface and depths below 2000 m. Their life history indicates that paralarval stage growth occurs in surface waters, and is followed by an ontogenetic migration to greater depths, where maturation takes place (Voss et al., 1992). *Liocranchia reinhardti* Steenstrup, 1856 is a fast growing species with a two-phase (depth-wise) life cycle (Arkhipkin, 1996). In the first phase, paralarvae, juveniles, and subadults can be found in epi and mesopelagic waters, between 0 and 500 m depth (Nesis, 1987), where they feed and grow up to about 170 to 200 mm ML in 4 to 5 months. Small paralarvae probably ascend to epipelagic waters after hatching, as confirmed by the capture of small (2.4 mm ML) individuals in superficial waters in the open tropical Atlantic (Arkhipkin et al., 1988). The second phase is characterized by a migration to deeper waters for maturation and subsequent spawning (Nesis, 1987; Arkhipkin, 1996).

Loliginids can be found all around the world, except in polar regions, but are usually limited to neritic waters within the shelf break. *Doryteuthis opalescens* Berry, 1911, which can be found from the surface up to 500 m within 200 miles from the shore, is endemic to the

California Current, ranging from the southern tip of Mexico (Baja California Peninsula, 22^{o}N) until southeastern Alaska (58^{o}N) (Jereb & Roper, 2010). Individuals are of small to medium size, averaging 140 to 170 mm ML (Jereb & Roper, 2010), and short lived, reaching maturity as early as 6 months (Butler et al., 1999) and living up to 10 months (Jackson, 1994). Koslow & Allen (2011) observed that paralarval abundance in near-surface waters was higher at night than during daytime, indicating a migration to the neuston at night.

The diversification of developmental modes and the evolutionary history of larvae have received little attention in cephalopods, but have a crucial role in understanding several biological processes. *C. veranyi* and *L. reinhardti* are key species for the understanding of evolutionary history of cephalopod paralarvae, as the morphological changes they go through between the paralarval and the juvenile/adult phases are the closest there can be to a metamorphosis in cephalopods. Morphological changes during ontogeny are much less pronounced in *D. opalescens*.

Studies on buccal structures of cephalopod paralarvae and their ontogenetic development are scarce in the literature and fundamental for a better understanding of their ecology. The beak, a chitinous structure found in the buccal mass, is a powerful feeding tool, which is used together with surrounding musculature for slicing small pieces of tissue from prey. It is composed of upper (UJ) and lower (LJ) jaws, which differ from each other both in morphology and in function (Raya & Hernández-González, 1998). Given its direct importance in feeding and in development, the beak (and its characteristics) of oceanic species with pronounced morphological changes during ontogeny, such as *C. veranyi* and *L. reinhardti*, can be contrasted with that of a coastal species, such as *D. opalescens.* Such comparison could, perhaps, provide opportunities for testing hypothesis about the diversification of developmental modes and evolution of cephalopod paralarvae. Thus, the aim of this study was to examine the morphology and morphometry of the beak structures of paralarvae of *C.* cf. *veranyi*, *L. reinhardti*, and *D. opalescens* during early ontogeny and to compare the most important structures between species. This information could shed light into the different developmental modes between oceanic and neritic species.

Material and Methods

Paralarvae of *Chiroteuthis* cf. *veranyi* from 3.62 to 13.62 mm mantle length (ML) and of *Liocranchia reinhardti* from 2.8 to 20.63 mm ML were sampled during various research cruises between 1984 and 1997off southern Brazil (28^{o}30’S – 34^{o}40’S) by plankton tows using 60-cm diameter and 300-µm mesh Bongo nets. Oblique tows were performed between the surface and approximately 300 m depth. Paralarvae were fixed in 4% formaldehyde.

Doryteuthis opalescens paralarvae from 2.25 to 12.30 mm ML were reared at the National Resources Center for Cephalopods (NRCC), University of Texas Medical Branch, Galveston, Texas (U.S.A.), by Dr. Érica Vidal between 1997 and 2000. The eggs were collected in spawning grounds on the coast of California and taken to the laboratory, where they were reared at 16 ± 1^{o}C from 1 to 70 days after hatching and fed a mixture of enriched *Artemia* sp. nauplii, wild copepods (various developmental stages), and mysid shrimps (*Americamysis almyra*) (Vidal et al., 2002a). Methodological details can be found in Vidal et al. (2002a, 2002b, 2006). All paralarvae were fixed and stored in neutralized 4% formaldehyde.

Extraction and storage of beaks of 18, 16, and 31 paralarvae of *C.* cf. *veranyi*, *L. reinhardti*, and *D. opalescens*, respectively, were performed according to Franco-Santos et al. (submitted).

Digital images of both upper (UJ) and lower (LJ) jaws were obtained with an Olympus SC20-GA camera coupled with an Olympus SZX7 stereoscopic microscope. Images had ventral and dorsal orientation for LJ and UJ, respectively, and measurements were taken using Image J version (Rasband, 1997) 1.46.

Morphological description of jaws was done through visual observations during and after image capture. The descriptions were made for size (ML) intervals, i.e., a specimen size (ML) was only described if morphological changes in either one of the jaws were observed from the previous size described, and only the jaw for which change was noticed was described. Measurements of structures were taken according to Franco-Santos et al. (submitted), with the exception of the base length (BL), which was excluded for being equal to the crest length (CL). A new structure was also added, the lower jaw width (LJW).

The UJ measurements (Fig. 1a) were: hood length (HL), the straight line between the rostrum anterior apex and the hood aboral extremity; rostrum length (RL), the straight line between the rostrum apex and the point in the jaw amplitude line that forms a 90° angle with the RL line; jaw amplitude (JA), the straight line joining the most external points in the jaw where rostrum protrusion begins; lateral wall aperture (LWA), the straight line between the most external points in the base of the lateral walls; upper jaw length (UJL), the straight line between the most external point in the posterior region of the jaw and the point where it forms a 90° angle with the LWA line; and upper jaw width (UJW), the straight line between the most external points in the lateral wall when looking at the dorsal region of the UJ.

The LJ measurements (Fig. 1b) were: HL, the straight line from the rostrum apex to the most posterior point of the hood; RL, the straight line between the rostrum apex to the point where it forms a 90° degree angle with the JA line, leading to negative values when a regression was observed instead of a protrusion; JA, the straight line joining the most external points in the jaw, where rostrum protrusion or dentition (if present) begins; wing aperture (WA), the straight line uniting the most internal points at the base of the wings, where these elevate to form the rostrum; wing length (WL), the straight line between the most anterior wing point and the point where the wing meets the lateral wall and begins its elevation to the hood region; wing width (WW), the straight line between the most external lateral points in the wing, from the point where the WA line ends (the internal-most part of the wing) to the point that delimits the external-most region of the wing (found with a tangent line to the most external point); crest length (CL), the straight line between the point in the JA line that forms a 90° angle with the tangent line to the most posterior point in the crest; and lower jaw width (LJW), the straight line between the most external lateral points in the lateral wall when looking at the LJ's ventral region.

Beak shape, size, coloration pattern (resulting from quinone tanning of the proteins associated with the chitin layers of the beak), structure and presence (number)/absence of teeth were analyzed for all species, and their beaks' morphology and morphometry were then compared. Arm crown development was also analyzed for the species – general characteristics are provided, mostly arm formula, number of suckers per arm, arm sucker diameter, and tentacle length. In the case of *C.* cf. *veranyi* and *D. opalescens* individuals of several sizes were analyzed and development was described according to size classes, while for *L. reinhardti* only one individual (10.88 mm ML) could be analyzed.

The relationship between the beak structures and overall individual growth was assessed by the model $\ln(Y) = \ln(a) + b_1 * \ln(X_1) + b_2 * \ln(X_2) + b_n * \ln(X_n) + e$, which was reduced using manual stepwise multiple linear regression, where the dependent variable is the ML, the regression parameters are the growth coefficient of each jaw structure, and the independent variables are the jaw structures. The structures that showed the highest influence on (i.e., better explanation of) growth were determined, together with the multiple linear regression equations, multiple determination coefficients (R^2), and F and *P* values. Transformed values (to conform to normality and homocedasticity assumptions) for each structure were compared between species through ANOVA and TukeyHSD (post-hoc) tests in order to determine possible differences among them. Some of the values obtained for the RL were negatives, and had to be transformed: values were substituted by the group's (RL) mean of a certain species if the amount of negative values was < 30% of total values; and substituted by 0.1 if the amount of negative values was > 30% of total values obtained. All statistical analyses were performed using R (Ihaka & Gentleman, 1993) version 2.13.0.

Results

Chiroteuthis cf. *veranyi*

A total of 18 beaks were extracted from paralarvae of *Chiroteuthis* cf. *veranyi*. Measurements were taken from 17 UJ and 17 LJ for all structures. Teeth were only present in the LJ, and could be spotted in 15 out of the 17 jaws examined (not observed in individuals with 5.63 and 5.75 mm ML).

1. Morphology

3.62 mm ML – UJ (Fig. 2a): teeth were not present, but there was a very pronounced slit in the rostrum area (uncollapsed jaw); jaw was not colored. LJ (Fig. 2b): moderately serrated teeth were present, and so was a very pronounced slit in the rostrum area; color pattern was light orange in the rostrum area and extended posteriorly in a narrow light yellow band (following the rostrum limits) toward the end of the hood. Both jaws were very fragile.

5.63 mm ML – UJ (Fig. 2c): the main changes were found in the slit, which has closed slightly. LJ (Fig. 2d): coloration became slightly more intense and could be seen also in the JA area.

6.13 mm ML – UJ (Fig. 2e): the slit was almost completely collapsed; the hood was still very fragile.

6.50 mm ML – UJ (Fig. 2f): jaw increased in length (anterior-posterior axis) and a protrusion developed in the rostrum, although a small slit was still perceptible; there was no coloration. LJ (Fig. 2g): jaw developed in size, although the elongate "cylindrical" form seen at this size (more common for individuals ≥ 11.86 mm ML) is distinct from the more round shape of the forthcoming smaller sizes; rostrum seemed to regress instead of protrude; the color pattern, in orange and light red color, darkened slightly, although it decreased in extension from the size previously described, i.e., it was apparent in the areas of the rostrum and anterior region of the hood but not in the JA and posterior region of the hood.

11.86 mm ML – LJ (Fig. 2h): the jaw developed in size; teeth eroded but were still visible in what seemed to be the beginning of protrusion of the rostrum; coloration was less intense (light orange) and still occupied a small area in the JA region and part of the hood; the slit did not collapse.

13.62 mm ML – UJ (Fig. 2i): no changes in shape and size, and the only noticeable change was the closure of the slit.

Throughout the ontogeny of the jaws of *C.* cf. *veranyi* (Fig. 2) it was possible to observe that no major changes occurred in the UJ – none of the examined ML sizes exhibited a color pattern; there was only a small protrusion of the rostrum; an increase in overall length (anterior-posterior axis); and the closure of the slit. In the LJ it was possible to see the beginning of a protrusion in the rostrum and a change in both form (from a more “round” to a more “cylindrical” shape) and in coloration intensity (from light yellow to light red) and extension (rostrum, JA, and hood), although the change in the latter was not progressive and retroceded at times; in all examined sizes the slit did not close during ontogeny. No clear dentition pattern was identified for the LJ, and teeth were not present in the UJ.

Arm-crown development: almost all individuals had one larger sucker at the base of each tentacle and smaller carpal suckers along the entire tentacle stalk. General arm formula and number of suckers on each arm (in parentheses) could be divided into two size categories: (a) 3.62 to 7.25 mm ML: arm formula = 2(2):1(2):4(1):3(0), sucker diameter was 31.25 µm (arm I of 3.62 mm ML paralarva), and tentacle length (TL) ranged from 1.4 to 4.38 mm; (b) 7.88 to 11.88 mm ML: arm formula = 4(3-7):2(3):1(2):3(0), sucker diameter ranged from 10 to 31.25 µm in arms IV of 9.5 and 11.88 mm ML paralarvae, respectively, and TL ranged from 4.13 to 13.75 mm. Arm III was poorly developed or rudimentary at times for both size categories. The 11.88 mm ML paralarva was described in more details for further comparison with similar sized individuals from the other species: arm formula = 4:2:1:3, mean sucker diameter of 25 and 31.25 µm (arms II and IV, respectively), 13.75 mm TL; tentacles with two rows of small carpal suckers and club with six rows of small (~ 12.5 µm diameter) suckers.

2. Morphometry

Results for the linear multiple regression on the UJ of *C.* cf. *veranyi* showed that the structures with highest indirect influence on paralarval growth (ML) (through feeding) were the UJL, LWA and UJW, respectively (Multiple linear regression, R^2 multiple = 0.72, $F_{(6,10)}$ =

4.33, *P* = 0.02). The results for the LJ showed that the structures with highest indirect influence on ML were the WL and LJW, respectively (Multiple linear regression, $R^2 = 0.59$, $F_{(8,8)} = 1.44$, *P* = 0.31). Parameters for the multiple linear regressions used to identify the growth relationship between these structures and the ML are shown in Table 1.

Liocranchia reinhardti

A total of 16 beaks were extracted from paralarvae of *Liocranchia reinhardti*. Measurements were taken from all 16 UJ and LJ for all structures. Teeth were present only in the LJ, in 4 out of 16 jaws examined (observed in individuals with 2.8, 5.5, 6.75, and 14.0 mm ML).

1. Morphology

2.8 mm ML – UJ (Fig. 3a): jaw was transparent; growth rings were clearly visible; a slit was observed in the rostrum and hood areas; there were no teeth. LJ (Fig. 3b): jaw was short and wide (noticeable by the wide WA); teeth were present; coloration was yellow and located in the rostrum, JA, and hood areas, forming a “T” pattern; a very small slit was present.

5.5 mm ML – UJ (Fig. 3c): no change in form, but there was a slight protrusion of the rostrum; the slit seemed to have collapsed, although the region was still fragile from having less chitin layers than the surrounding hood area. LJ (Fig. 3d): coloration darkened (orange color) in the hood area; slit was still visible.

6.13 mm ML – major changes have occurred in both jaws, which appear more like those of a juvenile than that of a paralarva. UJ (Fig. 3e): shape became more elongate (anterior-posterior axis); rostrum showed a considerable protrusion when compared to the previous size; dark red and orange colors occupied the rostrum and the anterior part of the hood (orange), forming a “V” pattern. LJ (Fig. 3f): the slit not only collapsed, as was observed in the previous size, but also developed into a rostrum; wings developed considerably, teeth were no longer present, but rather substituted by a much protruded rostrum; growth rings became visible; WA narrowed considerably; coloration intensified (dark orange, red, and dark red) and extended, occupying all of the rostrum and the anterior part of the hood, although a light-faded yellow color was visible in the posterior part of the hood.

9.13 mm ML – there was an overall increase in size for both jaws, although there were no major changes in form. UJ (Fig. 3g): the extension of the colored area increased slightly, occupying the inside region of the “V” pattern described previously (dark orange). LJ (Fig. 3h): coloration was similar to the previous size, but showed a “W” pattern.

20.00 mm ML – there was an overall increase in size for both jaws. UJ (Fig. 3i): protrusion of rostrum was much greater; coloration extended further into the posterior part of the hood, with intensity pattern decreasing in a “V” fashion from the dark red in the outer rostrum parts to the orange intermediate area of rostrum and hood and finishing in the dark yellow area of the mid-region in the anterior part of the hood. LJ (Fig. 3j): rostrum was much more protruded; rostrum area color was more intense (dark red).

During the development of *L. reinhardti*’s beak (Fig. 3) it was possible to observe major changes for both jaws, which seemed to develop up to an advanced paralarval/early juvenile stage within a short ML interval, from 5.5 to 6.13 mm. Coloration increased both in intensity, going from light-faded yellow to dark red tones, and in extension, from absent to encompassing the rostrum and part of the hood. Teeth were only observed in the LJ, although no dentition pattern could be identified, and were not present in paralarvae ≥ 6.13 mm ML, while rostrum protrusion occurred progressively throughout ontogeny. The slit in the rostrum was no longer apparent in the UJ and LJ of paralarvae ≥ 5.5 and ≥ 6.13 mm ML, respectively. In the LJ the wings showed a marked development in size and in vertical projection, which began to be noticed in larger MLs.

Arm-crown development was not evaluated for *L. reinhardti* individuals, but one individual sized 10.88 mm ML could be described: arm formula = 3:2:1:4, with mean sucker diameter of 181.8 (arm I); ~ 17.4 mm TL; tentacles with two rows of small carpal suckers along the tentacular stalk and club with four rows of small suckers, all of which measured ~ 90.9 µm in diameter;.

2. Morphometry

Results for the linear multiple regression on the UJ of *L. reinhardti* showed that the structures with highest indirect influence on paralarval growth (ML) were the LWA, UJW, and JA, respectively (Multiple linear regression, R^2 multiple = 0.78, $F_{(6,9)}$ = 5.22, *P* = 0.01). The results for the LJ of *L. reinhardti* showed that the structures with highest indirect influence on ML were the RL, JA, WA, and WW, respectively (Multiple linear regression, R^2 = 0.88, $F_{(8,7)}$ = 6.72, *P* = 0.01). Parameters for the multiple linear regressions used to identify the growth relationship between these structures and the ML appear in Table 1.

Doryteuthis opalescens

A total of 32 beaks were extracted from paralarvae of *Doryteuthis opalescens*, for which the age is also provided. Measurements were taken from 27 UJ and 28 LJ for all structures. Teeth were only present the LJ, and could be spotted in 27 out of the 28 jaws examined (not observed on the 10.25 mm ML individual).

1. Morphology

2.25 mm ML (1 day-old) – UJ (Fig. 4a): jaw had a cylindrical form and no colored area; there were no teeth; a slit was not visible, but the jaw seemed less chitinized in the region where the slit would have been present; growth rings were slightly visible. LJ (Fig. 4b): coloration was absent; teeth were markedly visible and so was a slit in the rostrum area; wings did not project vertically, but their length covered a good percentage of the jaw's length (antero-posterior axis).

3.56 mm ML (10 days-old) – UJ (Fig. 4c): a conspicuous slit appeared on the rostrum; the anterior-posterior axis elongated slightly, the hood developed slightly, and the growth rings were more visible. LJ (Fig. 4d): wings developed in width; the teeth and slit were still present, the latter being slightly wider than in the previous size; rostrum and mid-hood (antero-posterior axis) areas were colored, in light and dark yellow tones; growth rings became visible, but were not easily noticeable.

4.50 mm ML (25-30 days-old) – UJ (Fig. 4e): rostrum protruded (in contrast to previous sizes' round shape), and a small "V" pattern of light yellow color was observed restricted to its tip.

4.70 mm ML (30 days-old) – UJ (Fig. 4f): coloration developed in the rostrum (except for its outer region) and anterior part of the hood areas in a "V" pattern, which went from light and dark yellow to orange from the inner to the outer areas of the "V"; rostrum showed a greater protrusion; and hood was larger. LJ (Fig. 4g): jaw was elongated in the antero-posterior axis; dentition was still visible, although worn out; the rostrum protruded in an odd concave format, in which the external sides have projected forward but the inside region has not protruded; the slit was still very pronounced, and its opening seemed to increase from that of previous sizes, accompanying the development of the rostrum's protrusion; coloration intensified to orange and red tones, and extended to the posterior part of the hood, although still restricted to its mid-region; growth rings were clearly visible.

5.16 mm ML (35-40 days-old) – UJ (Fig. 4h): coloration extended to the rostrum's lateral region and advanced slightly to the hood area (towards its posterior region). LJ (Fig.

4i): hood was more developed, and the rostrum less concave, although no major changes could be observed in degree of protrusion; colored area extended from the mid-region of the hood to its sides, being present in the hood and rostrum in dark orange (most of the lateral regions) and red (mid of the rostrum and anterior part of the hood) tones.

5.43 mm ML (36-40 days-old) – UJ (Fig. 4j): rostrum was more protruded; jaw darkened (darker orange tones) and coloration increased slightly in extension in the hood, advancing towards its posterior region.

6.16 mm ML (46-50 days-old) – LJ (Fig. 4l): wings developed more than the jaw itself by a forward (anterior) extension in the antero-posterior axis, into what seemed to be the beginning of a vertical projection; rostrum protrusion was no longer concave, but rather narrow and more prominent, and showed red tones in its mid region; teeth and slit were still present.

12.30 mm ML (64 days-old) – UJ (Fig. 4m): jaw acquired an elongated form; rostrum was more protruded; extension of colored area did not change, although it was more intense, forming a “V” degradé color pattern, going from bright red in the lateral parts and dark red on the tip to orange and yellow in the interior portion of the “V”. LJ (Fig. 4n): the posterior part of the jaw became more cylindrical; wings showed a beginning of vertical projection; teeth were no longer present and the rostrum protruded and acquired a pointy shape, but the slit had not yet collapsed; rostrum coloration was stronger (bright red and dark orange) and occupied its entirety, forming a “W” pattern of darker outer parts and lighter inner parts.

Throughout the ontogeny of *D. opalescens*’s jaws (Fig. 4) it was possible to observe that teeth, which did not show a clear pattern, were only present in the LJ, and these disappeared between 6.16 and 12.30 mm ML. A slit was present only in the LJ (although a lower level of chitinization could also be noticed in the UJ), and was still visible in the LJ of paralarvae of 12.30 mm ML. Rostrum development was observed in both jaws, although it was accompanied by the persistence of the slit in the LJ. Wings developed in the LJ and their proportion to jaw length increased throughout ontogeny, and the beak elongated along its antero-posterior axis. Except for rostrum projection and increase in hood extension, there were no major changes in the UJ, and only the elongation of the beak in the antero-posterior axis, as seen in the LJ, could be observed. Growth rings could be observed in both UJ and LJ from paralarvae ≥ 2.25 and ≥ 3.57 mm ML, respectively. The color pattern for both jaws went from non-existing in newly-hatched paralarvae (2 days-old) to dark red and orange tones, although restricted to the rostrum and hood areas.

Arm-crown development was divided in three size categories: (a) 2.3 mm ML (1 day-old): arm formula = 3(5):4(2):2(1):1(0). The tentacles were easily discernible from the other arms and possessed about 18-20 suckers that were distributed along their entire length, and the tentacular clubs were not differentiated; (b) 3.5-5.0 mm ML (30 days-old): arm formula = 3(17):4(7):2(6):1(1), mean TL = 2.36 ± 0.3 mm. The length of arms and tentacles and the number of suckers on them increased considerably. On the arms, the suckers were distributed in two alternate rows as in the adults. The tentacles had about 38-40 suckers distributed in 4 rows, occupying about 70 % of the TL, clubs were not differentiated; (c) 12.30 mm ML (60 days-old): arm formula = 3(28):4(30):2(24):1(14); mean TL = 5.8 ± 0.83 mm. The tentacles had about 24 longitudinal rows of suckers and the suckers occupied approximately 60% of the TL, with a not well defined club. On the clubs, the four longitudinal sucker rows were already formed, but the dactylus was not yet differentiated.

2. Morphometry

Results for the linear multiple regression on the UJ of *D. opalescens* showed that the structures with highest indirect influence on paralarval growth (ML) were the HL, and UJW, respectively (Multiple linear regression, R^2 multiple = 0.95, $F_{(6,20)} = 64.97$, $P = 4.62*10^{-12}$). The results for the LJ showed that the structures with highest indirect influence on ML were the WL, WA, and CL, respectively (Multiple linear regression, $R^2 = 0.92$, $F_{(8,19)} = 26.1$, $P = 1.12*10^{-8}$). Parameters for the multiple linear regressions used to identify the growth relationship between these structures and the ML appear in Table 1.

Comparison between the UJ and LJ of *Chiroteuthis* cf. *veranyi*, *Liocranchia reinhardti* and *Doryteuthis opalescens*

1. Morphology

The development of the UJs occurred in distinct degrees for the three species. The smallest MLs of *Chiroteuthis* cf. *veranyi*, *Liocranchia reinhardti*, and *Doryteuthis opalescens* (3.62, 2.80, and 2.25 mm, respectively) were somewhat similar, in that they had an UJ of fragile aspect; transparent color; poorly developed hood and rostrum; presence of a slit in the rostrum of *C.* cf. *veranyi* and *L. reinhardti* (Figs. 5a and 5b); and a more round form (except for *D. opalescens*, which is only slightly cylindrical, Fig. 5c). In the larger individuals (13.62, 20.0, and 12.30 mm ML, respectively), however, they were no longer that similar, with the degree of development decreasing from *L. reinhardti* to *D. opalescens* and to *C.* cf. *veranyi*, respectively. Growth rings were visible on paralarvae ≥ 2.8 and ≥ 2.25 mm ML of *L. reinhardti* and *D. opalescens*, respectively – they were not observed in any of the sizes analyzed for *C.* cf. *veranyi*. A color pattern was not observed in *C.* cf. *veranyi*, and in *L. reinhardti* and *D. opalescens* it was restricted to rostrum and hood areas, being usually more intense in the outer regions of the rostrum and less intense in the interior regions of rostrum and hood. Rostrum protrusion was observed in all species, with a slight development in *C.* cf. *veranyi* (Fig. 5d) and a more intense one in *L. reinhardti* (Fig. 5e) and *D. opalescens* (Fig. 5f), respectively.

In the LJ the differences between species were more noticeable than observed for the UJ. The net morphological change in *C.* cf. *veranyi*, *L. reinhardti*, and *D. opalescens* between smaller (3.62, 2.80, and 2.25 mm ML) and larger (11.88, 20, and 12.30 mm ML) sizes (Figs. 6a through f), was again more pronounced in *L. reinhardti*, followed by *D. opalescens* and *C.* cf. *veranyi*. The smallest examined LJs were also fragile (although less than the UJ), round-shaped, and bore teeth and a slit in the rostrum area (Figs. 6a, 6b, and 6c, respectively). The smallest *C.* cf. *veranyi* and *L. reinhardti* already showed a color pattern, which was not observed in the smallest *D. opalescens*. In the largest individuals of *C.* cf. *veranyi* a negligible development of the wings, base (length of jaw), and rostrum was observed; the colored area showed to be slightly widespread. Contrariwise, the greatest sizes of *L. reinhardti* and *D. opalescens* showed a greater degree of coloration intensity and extension and a high level of wing and base development and of rostrum protrusion, such that their jaw looked more like that of a late paralarva/early juvenile than that of an early paralarva, the latter being the case for *C.* cf. *veranyi*. General level of rostrum development was distinct in the larger sizes - *L. reinhardti* showed a protruded rostrum in which the slit had already collapsed (Fig. 6d); *D. opalescens* no longer had teeth, but its protruded rostrum still had a slit (Fig. 6e); and *C.* cf. *veranyi* still had teeth and a slit (Fig. 6f). Growth rings were visible on paralarvae ≥ 6.13 and ≥ 3.57 mm ML of *L. reinhardti* and *D. opalescens*, respectively, and were not observed in any of the sizes analyzed for *C.* cf. *veranyi*.

A remarkable difference between the oceanic and neritic species can be found, however, if a comparison is made between individuals of *C.* cf. *veranyi*, *L. reinhardti,* and *D. opalescens* of a specific (similar) size, that of 5.75, 5.50, and 5.60 mm ML, respectively (UJ - Figs. 7a, 7b, and 7c, respectively; LJ - Figs. 8a, 8b, and 8c, respectively). This is the size after which it was possible to observe marked changes in the jaws of *L. reinhardti*. The observed differences suggest that drastic morphological changes occurred in the beak of *D. opalescens* earlier on than in *C.* cf. *veranyi* and *L. reinhardti*. On the other hand, comparing the larger paralarvae (11.88 mm ML for *C.* cf. *veranyi*, 12.13 mm ML for *L. reinhardti*, and 12.30 mm ML for *D. opalescens*) (Figs. 7d, 7e, and 7f for the UJ and 8d, 8e, and 8f for the LJ of the respective species), the UJs of *L. reinhardti* and *D. opalescens* resemble one another, the LJ of the former being more developed than that of the latter. Also, *L. reinhardti* and *D. opalescens* are more similar than are *D. opalescens* and *C.* cf. *veranyi* if comparing the LJ, the latter having shown an underdeveloped beak when compared to the other two. These morphological observation were not entirely supported by the ANOVA and post hoc results, in which the beaks of *C.* cf. *veranyi* and *D. opalescens* are similar to one another, especially for the LJs (Table 3), and that of *L. reinhardti* is completely different from these two, with the exception of a couple of jaw structures (Table 3).

2. Morphometry

Mean and standard deviation values for each jaw structure for the three species examined are shown in Table 2 and line graphs with mean and standard error bars are shown in Fig. 9. Results for ANOVA ($F_{(df1,df2)}$ and P) and post-hoc TukeyHSD (P for each species pairwise comparison) tests can be found in Table 3. All ANOVAs resulted significant. The structures of the UJ and LJ of *C.* cf. *veranyi* and *D. opalescens* were almost always similar, with the exception of ML, RL, and JA and of ML and HL, respectively. The beak structures of *L. reinhardti* were significantly different from those of both *C.* cf. *veranyi* and *D. opalescens*, with the exception of the LJ’s ML and of the UJ’s RL and LJ’s JA, respectively. The results indicate that the beaks of *C.* cf. *veranyi* and *D. opalescens* are morphometrically similar to each other, and that both are significantly different from that of *L. reinhardti*.

Discussion

The beak characteristics of the smallest paralarvae of *Chiroteuthis* cf. *veranyi*, *Liocranchia reinhardti*, and *Doryteuthis opalescens* were somewhat similar, i.e., they were fragile (the UJ more than the LJ), transparent or light colored (LJ of oceanic species), had poorly developed hood and rostrum, and showed teeth in the LJs and a slit in the rostrum of both UJ (in *C.* cf. *veranyi* and *L. reinhardti*) and LJ (all species). The development of the jaws occurred in distinct degrees for the three species, with differences being more noticeable in the LJs. The net morphological changes between smaller and larger sizes were greater for *L. reinhardti*, followed by *D. opalescens*, and by *C.* cf. *veranyi*, respectively.

It was hypothesized that species sharing similar environments and developmental modes, e.g. going through marked morphological changes during ontogeny, such as *C.* cf. *veranyi* and *L. reinhardti*, which live in oceanic waters and represent the closest there is to a metamorphosis in cephalopods, would have similar beak structures and that these would have a similar development. In this study this hypothesis was not verified either by the morphological or by the morphometric observations. The ANOVA results showed a higher morphometric similarity between the beaks of *C.* cf. *veranyi* and the neritic *D. opalescens*, and the morphological observations indicated that the beak of *D. opalescens* is more similar to that of *L. reinhardti* than to *C.* cf. *veranyi*. The difference in beak morphology observed between these oceanic species could perhaps be due to evolutionary history or to a specialization for a certain prey type (a beak more or less developed to feed on a hard or soft-bodied prey, for example), such that a distinct beak morphology and development would be related to the feeding habit rather than the environment occupied.

Ontogenetic migrations are performed by both *C.* cf. *veranyi* (Young & Roper, 1998; Jereb & Roper, 2010) and *L. reinhardti* (Nesis, 1987; Arkhipkin, 1996), which descend from the first hundred meters to greater depths for maturation, but are not a part of the life cycle of *D. opalescens*. Given the depth difference at which different life stages can be found, it is to expect that great morphological differences will accompany development, and that a marked alteration in beak characteristics could indicate a transition between stages and/or environments. That being said, it is possible that the sizes examined for *C.* cf. *veranyi* are representatives of a single life stage, since no major changes were observed, and that those examined for *L. reinhardti* encompass at least some ontogenetic and/or environmental change, perhaps from a paralarval to an early juvenile stage.

It is known that comparisons should be standardized by age or size, even though the determination of age in wild paralarvae is somewhat problematic and size (i.e., the standard measurement ML) might also not be an adequate parameter for comparisons (Vecchione, 1998), because of the influence of temperature on growth rate during ontogeny (Forsythe, 1993). Species or individuals growing under higher temperatures will usually develop faster than those under lower temperatures (O’Dor et al., 1982 and Caverivière et al., 1998 for eggs of *Illex illecebrosus* and *Octopus vulgaris*, respectively; Moltschaniwskyj & Martínez, 1998 for juvenile *Sepia elliptica*; and Vidal et al., 2002b for *Doryteuthis opalescens* paralarvae), and it could be that the level of beak development reflects environmental temperatures during ontogeny rather than pace of development. In the present study it was possible to observe a few individuals of *C.* cf. *veranyi* and *L.reinhardti* that had a less developed beak than that of smaller conspecifics, an observation that supports the view that size is not a good standardization method, especially for development comparisons. Hatching size for wild and reared *D. opalescens* has been reported from 2.5 to 3.2 mm ML (Vidal et al., 2002a, 2002b; Jereb and Roper, 2010), but is unknown for both *C.* cf. *veranyi* and *L. reinhardti,* although small paralarval sizes such as 2.4 mm ML have been observed for the latter in superficial waters (Arkhipkin et al., 1988), indicating that the smallest size evaluated in this study (2.80 mm ML) could be closer to the hatching size of *L. reinhardti*.

The quinone tanning of the proteins associated with chitin layers (added throughout development), which confers the coloration pattern (also referred to as pigmentation) of cephalopod beaks, is a continuous process (Clarke, 1980) and one of the most important changes in beak development (Mangold & Fiorini, 1966). The darker the color of the jaws, the harder and more robust the beak will be (Castro & Hernández-García, 1995; Hernández-García et al., 1998), and thus the greater the individual's ability to prey on larger, stronger, and harder prey. Beak strength will thus affect prey choice and feeding habit in general (Castro & Hernández-García, 1995), and in that sense the color pattern could be an indication of the type of prey ingested. A color pattern was not observed in the UJ of any *C.* cf. *veranyi* specimens, and although it was present in the LJ it was very light and restricted, indicating that this species has a very fragile beak in sizes up to 13.62 mm ML. A development in coloration was observed for both *L. reinhardti* and *D. opalescens* (although it involved only hood and rostrum areas), showing that during development their beak becomes stronger, possibly allowing the ingestion of larger and stronger prey. Underdeveloped beaks of paralarvae, such as the ones herein observed, will always have very fragile, flexible, and transparent edges, for these are growing regions (Hernández-García, 2003).

From the three species analyzed, *C.* cf. *veranyi* is the one with the lowest apparent beak development. This could be due to a series of reasons, such as the *Doratopsis* stage, an almost metamorphosis-like event in the species life history which is not fully understood and has an unknown duration (Young, 1991). Paralarvae can reach sizes up to 90 mm ML (Jereb & Roper, 2010) and 'larval' features seem to be retained up to at least 76 mm ML in some species (Roper & Sweeney, 1992), which indicates that the maximum ML examined in the present study (13.62 mm ML) could be attributed to an early paralarvae, although hatching size is unknown. It could be that, at such ML, paralarvae have yet much to develop and would exhibit an only slightly developed beak. Adult chiroteuthids have characteristically small and weak muscled mantles (Roper & Young, 1975), which would also imply that these squids are not voracious predators and should have slow growth rates and low metabolism. Additionally, their fragile and less developed beak could possibly reflect a diet on soft-bodied prey or even the occurrence of external pre-digestion of prey.

The low food incidence recorded for cranchiids (50 to 200 mm ML) from the Gulf of Mexico suggested that they might have a somewhat inactive life strategy (Passarella & Hopkins, 1991), which could perhaps also be inferred from a less firm musculature when comparing to other squids. This lower activity level would be accompanied by a reduced metabolic rate and by lower caloric demands (Passarella & Hopkins, 1991), thus they would not need to feed as frequently as other species. The results of the present study do not support entirely these considerations, since the observations on beak development of *L. reinhardti* show that between 5.5 and 6.13 mm ML there were marked changes in beak morphology and morphometry, indicating fast growth and, perhaps, that this could be a transition size. Also contradicting the relatively inactive life strategy theory is the work of Arkhipkin (1996), which states that *L. reinhardti* is among the fastest growing species in epipelagic waters of the tropical Atlantic.

The development of beak structures in *D. opalescens* was verified to occur very fast within the first 2 months of life, and although there is no information on age for the other two oceanic species, the beak of their smallest paralarvae did not show such a fast growth. A marked change, similar to what was observed for *L. reinhardti* but not so sharp, occurred between 4.50 and 4.70 mm ML. This could, perhaps, indicate a shift in prey size and type that the squid were able to capture. Nonetheless, this matter requires further investigation.

The analysis of the arm-crown structure can also serve as an unmistaken indication of how adapted an individual/species is to feeding on prey that is harder to catch and to hold on to. If we compare specimens of similar size, 11.88 mm and 10.88 mm ML for *C* cf. *veranyi* and *L. reinhardti*, respectively, we have that the development of the arm-crown complex is greater in the latter, which possesses longer tentacles and arms bearing larger suckers. This suggests that *L. reinhardti* may have a greater ability for grabbing and holding a prey, while *C.* cf. *veranyi* would not necessarily need a strong arm-crown to hold its prey at this size. The arm-crown of the *D. opalescens* paralarva of 12.30 mm ML was found to be more developed than that of both *C.* cf. *veranyi* and *L. reinhardti*, although the tentacles of the former were shorter than those of the other two species.

The multiple linear regression revealed that the UJ’s lateral walls (UJL and UJW) and hood (HL) and the LJ’s wings (WL, WW, WA) and lateral walls (CL and LJW) were, in general, the most robust structures for all species, with rostrum related structures (RL and JA) also playing a significant role in both jaws of *L. reinhardti*, and LWA being important for the UJ of the oceanic species. A rapid increase in size of hood (UJ), wings (similar function in the LJ as that of the hood – Boucaud-Camou & Boucher-Rodoni, 1983), and lateral walls can be expected in paralarvae (Hernández-García et al., 1998), given that these are areas of muscle attachment (Uyeno and Kier, 2007) and, thus, affect positively on beak strength. All beak structures, including those herein defined as more important for feeding and growth (except for the WA), had higher mean values in specimens of *L. reinhardti*, suggesting that this species has a more functional beak and, especially, rostrum. Such characteristics are likely reflected in the diet of *L. reinhardti* paralarvae, as has been mentioned by Boletzky (1971) for juvenile cephalopods and verified on *Illex coindetti* juveniles and adults by Castro & Hernández-García (1995). Rostrum development, together with coloration level, has also been suggested as having an important impact on diet choice for *Octopus vulgaris* (Hernández-García et al., 1998).

The growth of the rostrum has been described as comparatively slower than that of other structures, such as hood and lateral walls (Hernández-García et al., 1998), given its erosion throughout life and relatively specific use according to each species. In *C.* cf. *veranyi* the protrusion of the rostrum could be considered negligible, with the LJ still showing teeth and an intruded rostrum, indicating that this structure likely does not have a crucial function for the size range analyzed for this species. The rostrum in *L. reinhardti*, whose growth is significantly different from that of *C.* cf. *veranyi*, shows a marked protrusion from 5.5 to 6.13 mm ML for both UJ and LJ, a change accompanied by a strengthening of the structure through the addition of chitin layers. The species also had the largest mean values for RL, indicating that the rostrum has a fast growth during early ontogeny. In *D. opalescens* the jaws seem to develop in a rather uncoupled fashion, i.e. they show different degrees of development, such that they are not so different from *L. reinhardti*'s UJ and from *C.* cf. *veranyi*'s LJ. Changes in its UJ can be seen in paralarvae ≥ 4.50 mm ML, which already show a slight rostrum protrusion and whose slit has already collapsed, although coloration is still absent, while such changes in the LJ only happen between 6.16 and 12.30 mm ML, a range for which no paralarvae were examined, so a more specific size cannot be inferred for it. The observation of a faster development of the beak of *L. reinhardti* and of the UJ of *D. opalescens* could be related to the species' feeding habits, perhaps requiring a more prominent function of the rostrum. The LJ and UJ of *Octopus vulgaris* adults are different from one another not only in morphology, but also in function, such that the LJ supports the muscles controlling the movements of the UJ, which in turn will slice the food while moving over the former (Raya & Hernández-González, 1998). Accordingly, a greater development in the rostrum of the UJ in comparison to that of the LJ could be expected, since the former is the one cutting through the prey's flesh. Although little is known on the feeding habits of paralarvae of *L. reinhardti* and *D. opalescens*, the reason for such a differential rostrum development should not lie further from this, although more studies are required.

This is the first study to observe dentition in paralarvae of *C.* cf. *veranyi* and of *L. reinhardti*. In both species teeth were only present in the LJ, being visible throughout all sizes analyzed in the former and disappearing in paralarvae ≥ 6.13 mm ML in the latter. In *D. opalescens* teeth were also present in the LJ, and disappeared between 6.16 and 12.30 mm ML. A dentition pattern could not be identified for the three species. Teeth have also been observed in the LJ of paralarvae of Brachioteuthidae (Young et al., 1985) and Ommastrephidae (Wakabayashi et al., 2002; Shigeno et al., 2001) and in both jaws of Octopodidae (Boletzky, 1971; Nixon and Mangold, 1996; Nixon and Young, 2003; Franco-Santos et al., submitted), Argonautidae (Franco-Santos et al., submitted) and Loliginidae (Boletzky, 1974). According to Harman and Young (1985), if dentition occurs, it will wear off and disappear after the post-hatch growth phase, and the results obtained in the present study seem to confirm this – the beak of the largest *C.* cf. *veranyi* individual was still fragile and poorly developed, displaying teeth, while that of *L. reinhardti* showed a marked transition between the sizes of 5.5 and 6.13 mm ML, during which teeth were lost. There are a few hypotheses to explain teeth function in paralarvae, such as rapid discard of planktonic prey (Boletzky, 1974), and removal of semi-digested prey (crustacean) meat from exoskeleton in adult *Idiosepius paradoxus* (Kasugai et al., 2004), *O. vulgaris* paralarvae (Hernández-García et al., 2000), and *Loligo vulgaris* (Boletzky, 1974).

The presence of a slit in the rostrum of the both UJ and LJ could be noticed in all species examined (Figs. 7 and 8). In *C.* cf. *veranyi*, the slit collapsed in the UJ of the largest paralarvae (13.62 mm ML), but was still visible in the LJ; in *L. reinhardti* it collapsed in the UJ and LJ already in small paralarvae (≥ 5.5 and ≥ 6.13 mm ML, respectively). In *D. opalescens*, for which a slit was only present in the LJ, it did not collapse even in paralarvae of 12.30 mm ML. The presence of a slit has also been observed in the rostrum of the LJ of *Argonauta nodosa* and *Octopus vulgaris* paralarvae (Franco-Santos et al., submitted) and throughout the crest on the UJ of *Illex argentinus* paralarvae (Vidal & Bainy, pers. comm.). The slit collapsed in paralarvae of both *A. nodosa* (≥ 4.71 mm ML) and *I. argentinus* (≥ 3 to 4 mm ML), but was still visible in *O. vulgaris* from 1.68 to 3.63 mm ML.

The slit found in both jaws has been associated to characteristics of fossil cephalopod species (Franco-Santos et al., submitted), more specifically of those belonging to the *aptychus* morphotype of ammonoids, described by Lehmann (1981) as possessing a groove in the anterior region (crest) of the externally calcified LJ and an anteroposterior division of the UJ into two lateral walls. Teeth on the LJ were also characteristic of some ammonoids, although this is only briefly discussed by Tanabe and Landman (2002). More studies are needed in order to investigate why beak characteristics of ancestral cephalopods would be retained in early life stages of modern species and if they are related to paralarval feeding. It is possible that the collapse of the slit is related to a transition in diet for both *C.* cf. *veranyi* and *D. opalescens* and a diet shift for *L. reinhardti*, the only species for which it was possible to see the collapsing of the slit in both jaws.

Future research on the ontogenetic changes of beak morphology and on general paralarval feeding ecology would benefit from isotopic approaches, since these can be used to identify trophic position within a foodweb (δ^{15}N) and feeding mode (benthic vs. pelagic), habitat (offshore vs. inshore), and migration patterns (δ^{13}C) (Cherel & Hobson, 2007; Cherel et al., 2009). A complete dietary record of an individual can be obtained from sequential isotopic profiles of its gladius, which is able to retain feeding information of the entire life span (Lorrain et al., 2011). Phylogenetic approaches would also improve knowledge on this area by taking into account evolutionary context, allowing for comparisons of structure development and evolution.

Studies on the ontogenetic development of the beak in cephalopod paralarvae can provide new perspectives for understanding their ecology (Hernández-García, 2003) and also for unraveling higher-level systematic relationships, of which the patterns of teeth serration are particularly promising (Vecchione, 1998). This type of information is also important for a greater knowledge of paralarvae feeding ecology and behaviour and for understanding developmental modes and adaptations of cephalopods throughout evolutionary time.

Conclusions

Dentition was present in the LJs of all *Chiroteuthis* cf. *veranyi*, and in *Liocranchia reinhardti* and *Doryteuthis opalescens* paralarvae < 6.13 and ≤ 6.16 mm ML, respectively, but none of the species showed a clear dentition pattern. All beak structures that supposedly have an important role in paralarval feeding (UJ's hood and lateral walls and LJ's wings and lateral walls) were more developed in *L. reinhardti*, a species in which the rostrum structures were also important for determining ML, i.e. they contributed significantly to growth. The results suggest that rostrum functionality, which seemed greater for *L. reinhardti*, intermediate for *D. opalescens*, and lower for *C.* cf. *veranyi*, could be related to prey type, although further studies are necessary to confirm this. The UJ and LJ showed different development, and morphological changes in the beak structures occurred at distinct MLs for the three species. The color pattern varied slightly between *L. reinhardti* and *D. opalescens*, which showed a darkening of jaws with growth, while *C.* cf. *veranyi* showed very little color on the LJ and none in the UJ. The presence of teeth on the LJ and of a slit on the rostrum of both jaws of paralarvae of the three species may be related to ancestral beak characteristics. The results of this study reveal important information on the beak's functional morphology during the first stages of the life cycle, which are vital for understanding paralarval feeding ecology and overall adaptation throughout evolutionary time.

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Figure captions

Figure 1: Schematic drawing of paralarval upper and lower jaws. (a) Upper jaw, dorsal view: HL = hood length; RL = rostrum length; JA = jaw amplitude; LWA = lateral wall aperture; UJL = upper jaw length; UJW = upper jaw width. (b) Lower jaw, ventral view: HL = hood length; RL = rostrum length; JA = jaw amplitude; WA = wing aperture; WL = wing length; WW = wing width; CL = crest length. Paralarval teeth are indicated in both (a) and (b). Scale bar = 100µm.

Figure 2: *Chiroteuthis* cf. *veranyi*. Schematic drawing of the development of the upper (a, c, e, f, i) and lower (b, d, g, h) jaws of paralarvae. (a, b) 3.62 mm ML; (c, d) 5.63 mm ML; (e) 6.13 mm ML; (f, g) 6.50 mm ML; (h) 11.88 mm ML; (i) 13.62 mm ML. Scale = 100 µm

Figure 3: *Liocranchia reinhardti*. Schematic drawing of the development of the upper (a, c, e, g, i) and lower (b, d, f, h, j) jaws of paralarvae. (a, b) 2.80 mm ML; (c, d) 5.50 mm ML; (e, f) 6.13 mm ML; (g, h) 9.13 mm ML; (i, j) 20.00 mm ML. Scales: (a - d) = 100 µm and (e - j) = 200 µm

Figure 4: *Doryteuthis opalescens*. Schematic drawing of the development of the upper (a, c, e, f, h, j, m) and lower (b, d, g, i, l, n) jaws of paralarvae. (a, b) 2.25 mm ML; (c, d) 3.57 mm ML; (e) 4.50 mm ML; (f, g) 4.70 mm ML; (h, i) 5.16 mm ML; (j) 5.43 mm ML; (k) 6.16 mm ML; (l, m) 12.30 mm ML. Scales: (a - l) = 100 µm and (m, n) = 200 µm

Figure 5: Comparison of upper jaws of paralarvae of *Chiroteuthis* cf. *veranyi* (a, d), *Liocranchia reinhardti* (b, e), and *Doryteuthis opalescens* (c, f). (a) 3.62 mm ML; (b) 2.80 mm ML; (c) 2.25 mm ML; (d) 11.88 mm ML; (e) 20.00 mm ML; (f) 12.30 mm ML. Circles in a and b indicate the slit in the rostrum. Scale bars: (a - d) = 100 µm, (e) = 500 µm, and (f) = 200 µm

Figure 6: Comparison of lower jaws of paralarvae of *Liocranchia reinhardti* (a, d), *Doryteuthis opalescens* (b, e), and *Chiroteuthis* cf. *veranyi* (c, f). (a) 2.80 mm ML; (b) 2.25 mm ML; (c) 3.62 mm ML; (d) 20.00 mm ML; (e) 12.30 mm ML; (f) 13.62 mm ML. Circles in a-c, e, and f indicate the slit in the rostrum. Scale bars: (a - c, f) = 100 µm, and (d, e) = 200 µm

Figure 7: Comparison of upper jaws of paralarvae of similar mantle length (ML) of *Chiroteuthis cf) veranyi* (a, d), *Liocranchia reinhardti* (b, e), and *Doryteuthis opalescens* (c, f). (a) 5.75 mm ML; (b) 5.50 mm ML; (c) 5.60 mm ML; (d) 11.88 mm ML; (e) 12.13 mm ML; (f) 12.30 mm ML. Scale bars = (a - d) = 100 µm, and (e, f) = 200 µm

Figure 8: Comparison of lower jaws of paralarvae of similar mantle length (ML) of *Chiroteuthis cf) veranyi* (a, d), *Liocranchia reinhardti* (b, e), and *Doryteuthis opalescens* (c, f). (a) 5.75 mm ML; (b) 5.50 mm ML; (c) 5.60 mm ML; (d) 11.88 mm ML; (e) 12.13 mm ML; (f) 12.30 mm ML. Scale bars = (a - d) = 100 µm, and (e, f) = 200 µm

Figure 9: Mean values and standard error (bars) of each beak structure measured in the UJ (a - g) and LJ (h - q) of *Chiroteuthis* cf. *veranyi*, *Doryteuthis opalescens*, and *Liocranchia reinhardti*. (a) ML; (b) HL; (c) RL; (d) JA; (e) LWA; (f) UJL; (g) UJW; (h) ML; (i) HL; (j) RL; (l) JA; (m) WL; (n) WW; (o) WA; (p) CL; (q) LJW.

Figures

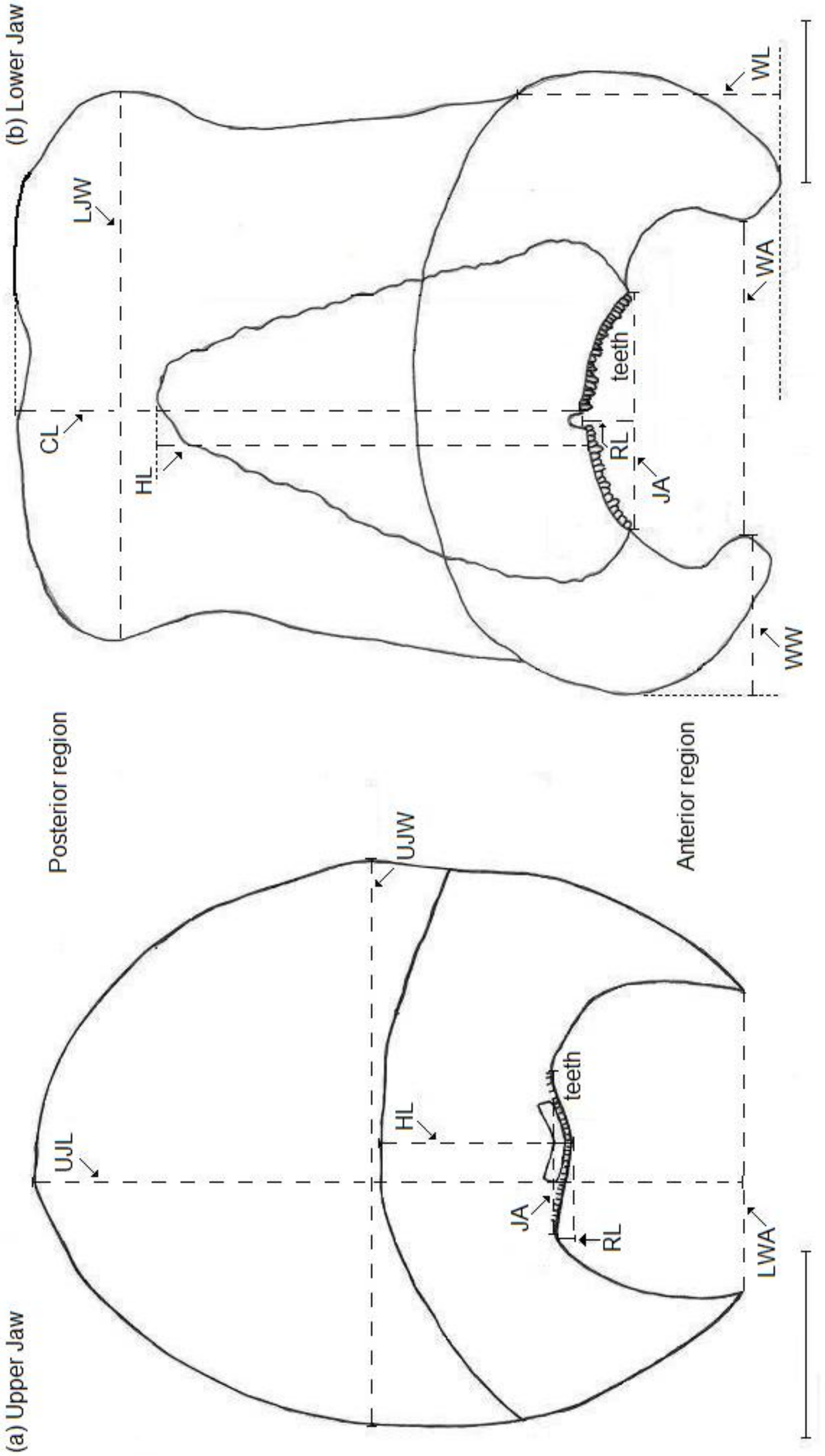
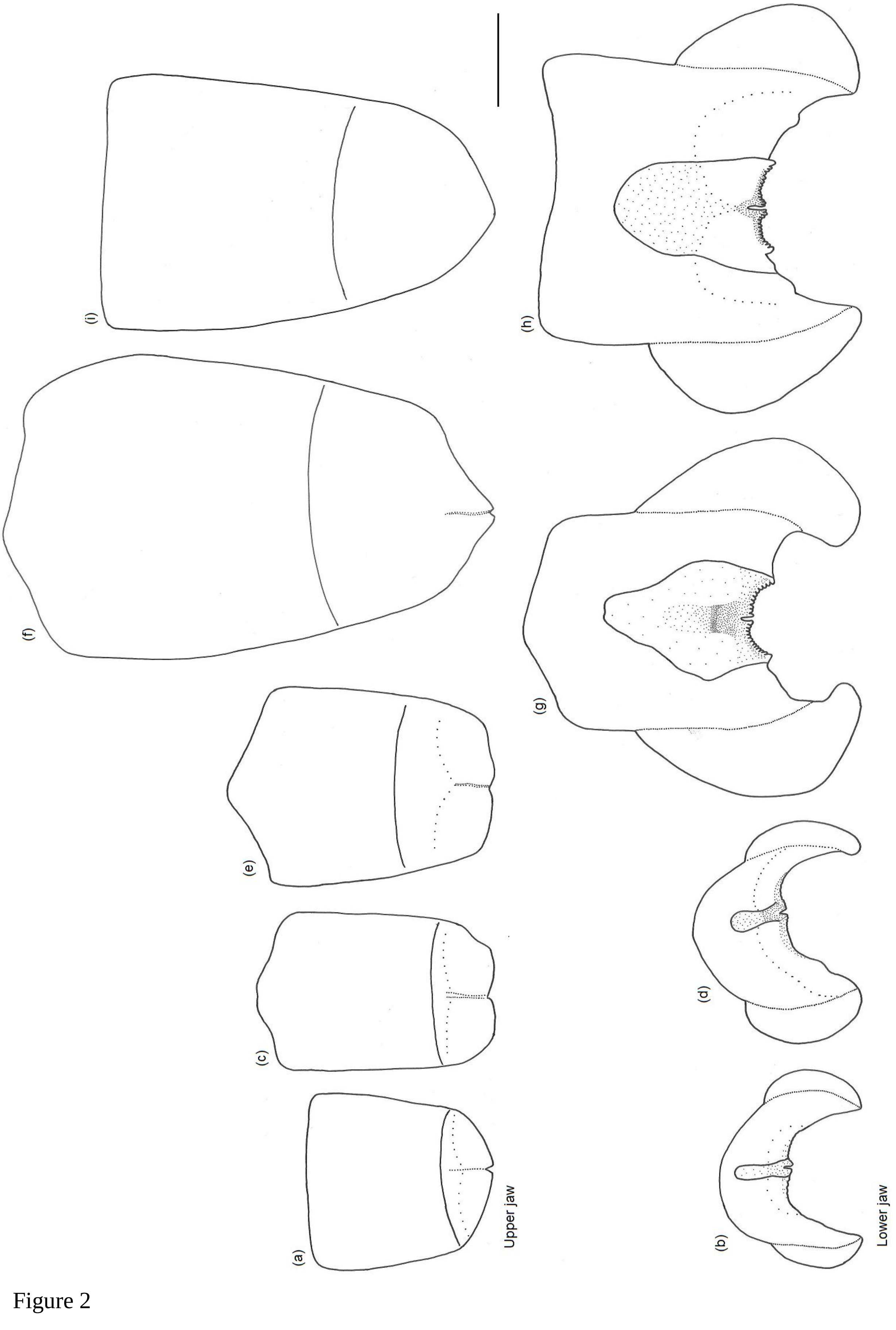


Figure 1



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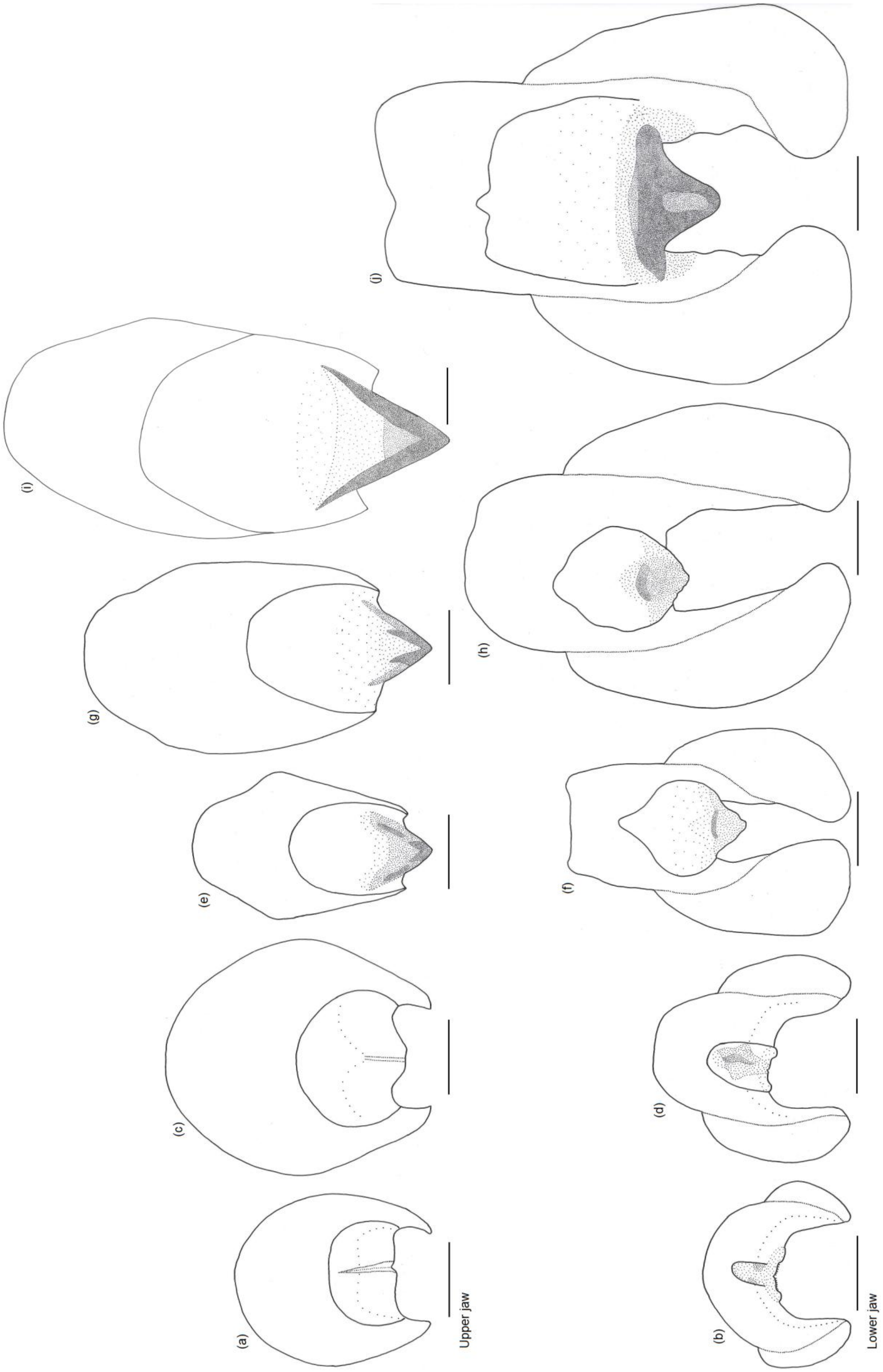

Figure 3

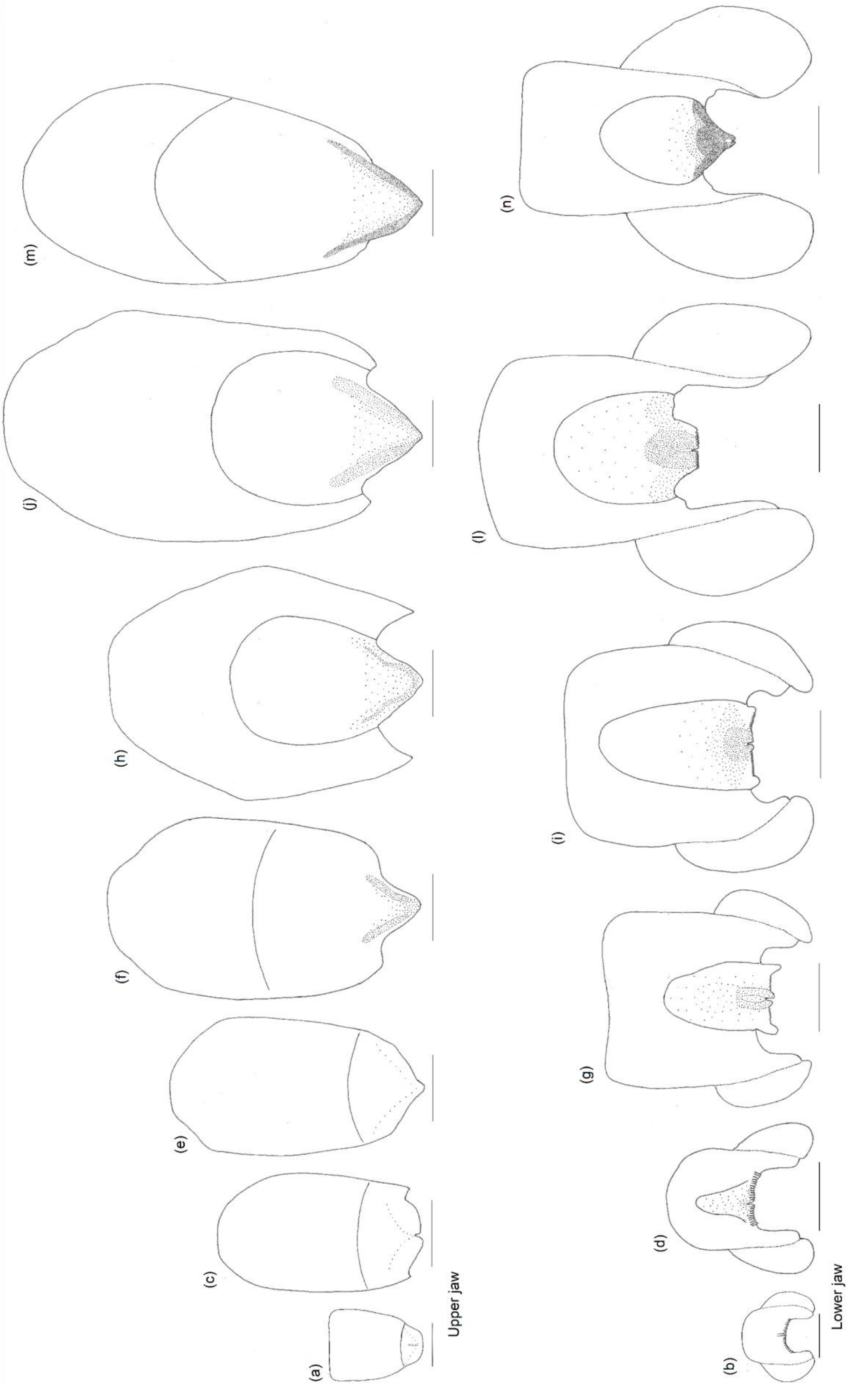

Figure 4

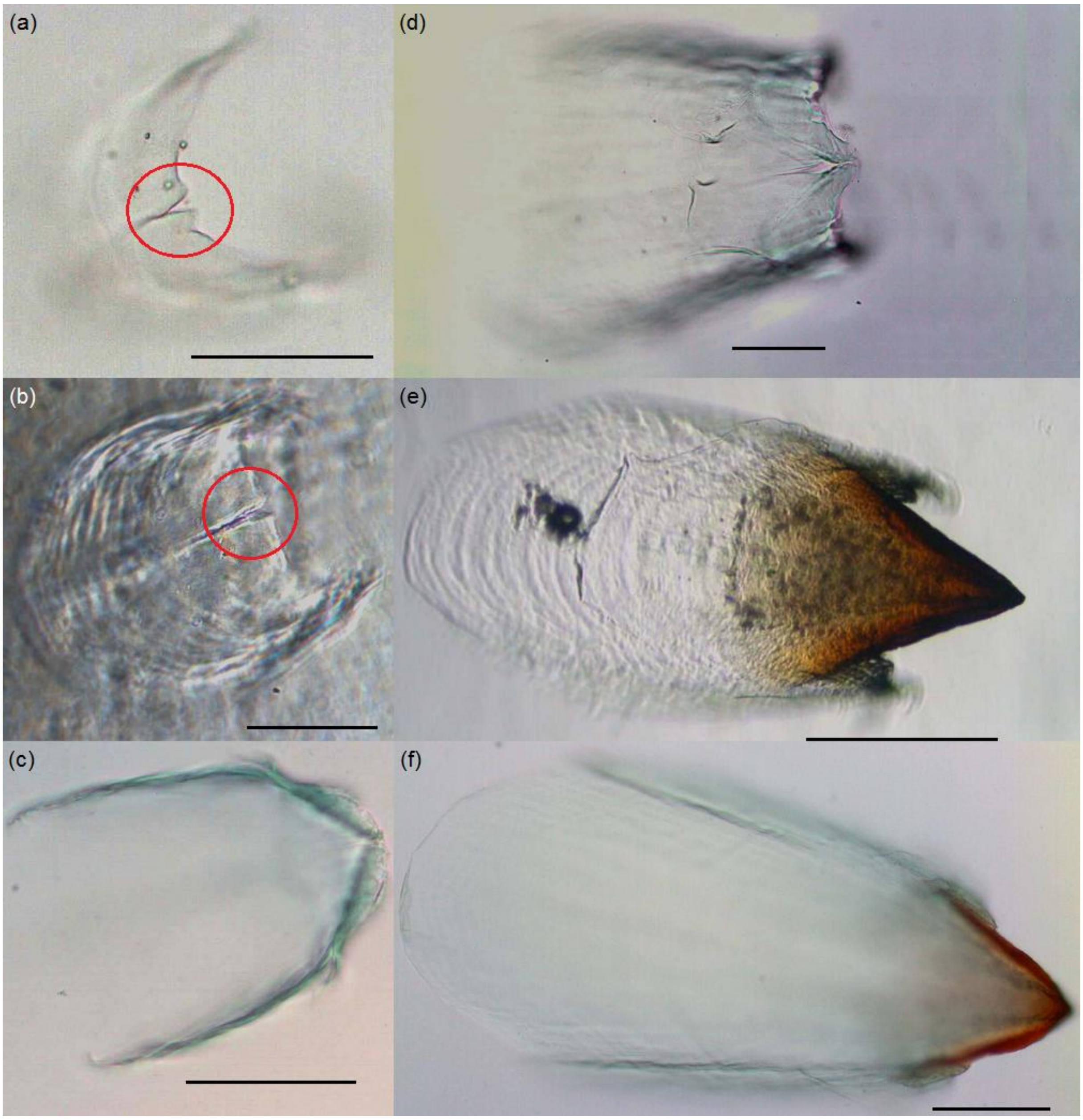

Figure 5

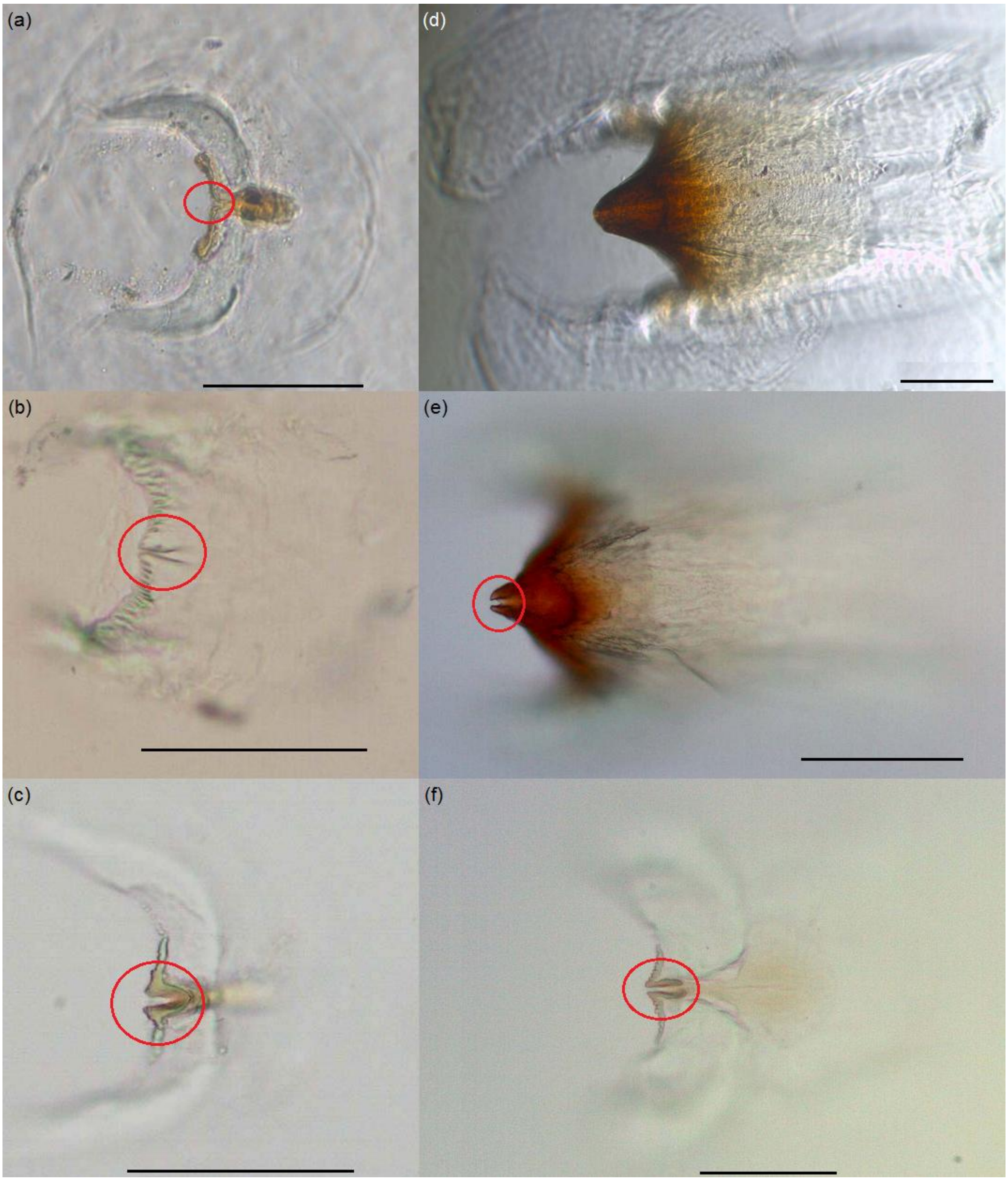

Figure 6

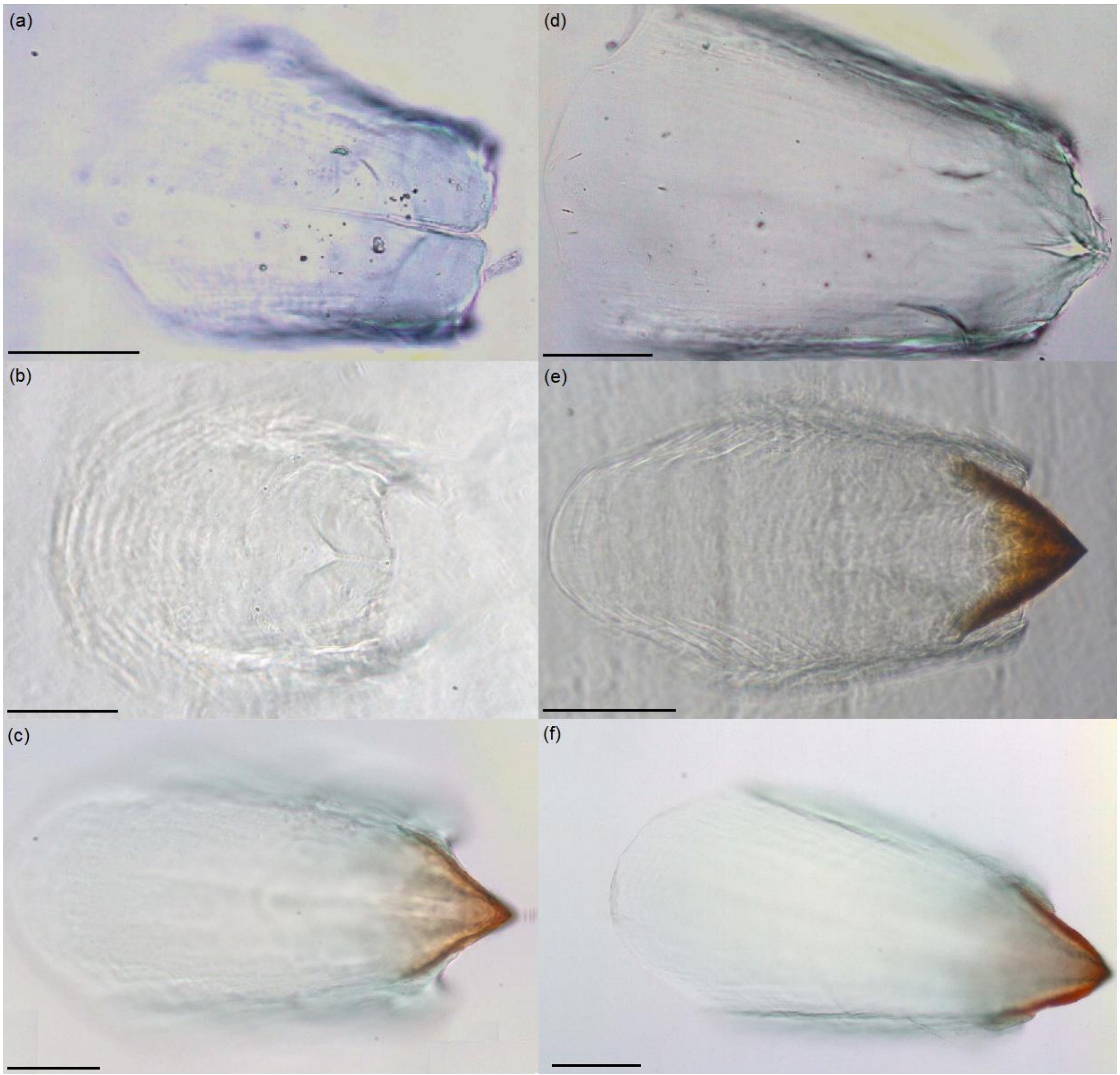

Figure 7

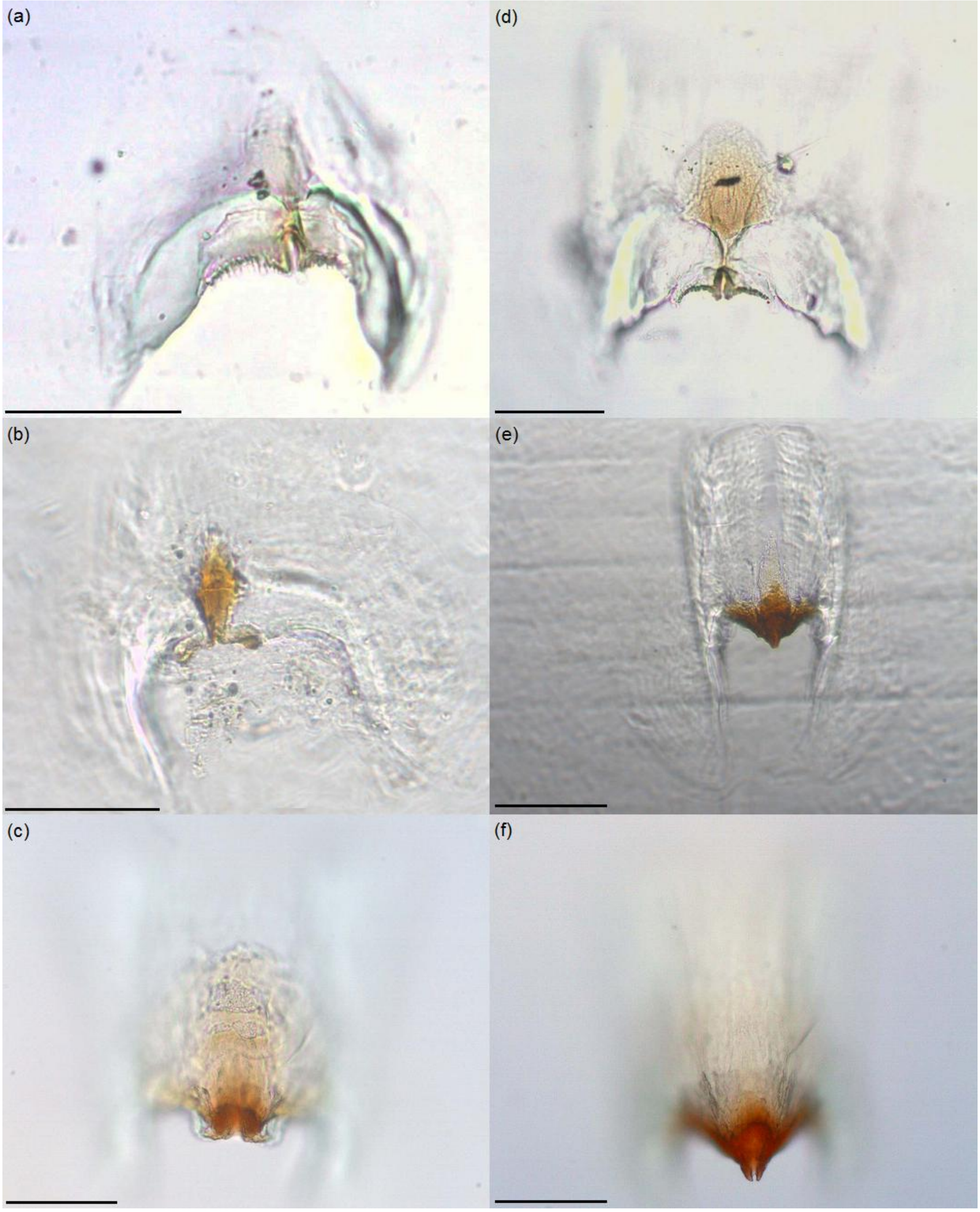

Figure 8

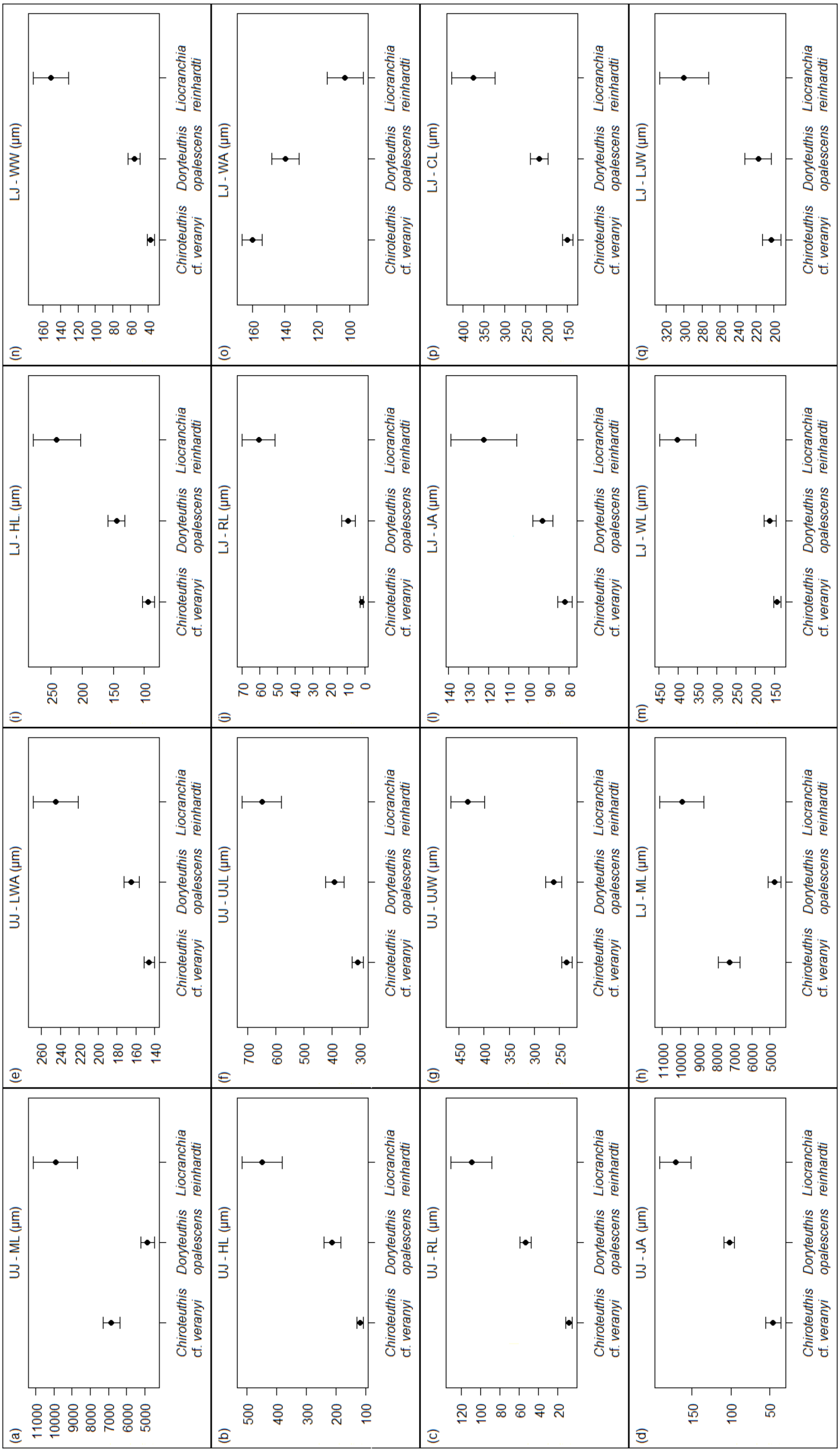
(a) UJ - ML (µm)
11000 10000 9000 8000 7000 6000 5000
(b) UJ - HL (µm)
500 400 300 200 100
(c) UJ - RL (µm)
120 100 80 60 40 20
(d) UJ - JA (µm)
150 100 50
(e) UJ - LWA (µm)
260 240 220 200 180 160 140
(f) UJ - UJL (µm)
700 600 500 400 300
(g) UJ - UJW (µm)
450 400 350 300 250
(h) LJ - ML (µm)
11000 10000 9000 8000 7000 6000 5000
(i) LJ - HL (µm)
250 200 150 100
(j) LJ - RL (µm)
70 60 50 40 30 20 10 0
(l) LJ - JA (µm)
140 130 120 110 100 90 80
(m) LJ - WL (µm)
450 400 350 300 250 200 150
(n) LJ - WW (µm)
160 140 120 100 80 60 40
(o) LJ - WA (µm)
160 140 120 100
(p) LJ - CL (µm)
400 350 300 250 200 150
(q) LJ - LJW (µm)
320 300 280 260 240 220 200
Chiroteuthis cf. veranyi
Doryteuthis opalescens
Liocranchia reinhardti

Figure 9

Tables

Table 1 Parameters for the manual stepwise multiple linear regression that determined the growth relationship between the upper (UJ) and lower (LJ) jaw structures and mantle length (ML) for *Chiroteuthis* cf. *veranyi*, *Liocranchia reinhardti*, and *Doryteuthis opalescens*. HL = hood length; RL = rostrum length; JA = jaw amplitude; UJL = upper jaw length; UJW = upper jaw width; WA = wing aperture; WL = wing length; WW = wing width; CL = crest length; LJW = lower jaw width.

Species	Jaw	N	Most important structures	Equationn	R^2	$F_{(df1,df2)}$	*P*
C. cf. *veranyi*	UJ	17	UJL (1st), LWA (2nd), UJW (3rd)	$\ln ML = 2.56 - 0.87\ln UJL - 1.12\ln LWA + 3.07\ln UJW$	0.72	$4.33_{(6,10)}$	0.02
C. cf. *veranyi*	LJ	17	WL (1st), LJW (2nd)	$\ln ML = 2.06 + 0.57\ln WL + 0.74\ln LJW$	0.59	$1.44_{(8,8)}$	0.31
L. reinhardti	UJ	16	LWA (1st), UJW (2nd), JA (3rd)	$\ln ML = 0.21 + 1.06\ln LWA + 1.37\ln UJW - 1.01\ln JA$	0.78	$5.22_{(6,9)}$	0.01
L. reinhardti	LJ	16	RL (1st), JA (2nd), WA (3rd), WW (4th)	$\ln ML = 4.06 - 0.17\ln RL - 0.54\ln JA + 0.50\ln WA + 1.22\ln WW$	0.88	$6.72_{(8,7)}$	0.01
D. opalescens	UJ	27	HL (1st), UJW (2nd)	$\ln ML = 3.69 + 0.19\ln HL + 0.68\ln UJW$	0.95	$64.97_{(6,20)}$	$4.62*10^{-12}$
D. opalescens	LJ	28	WL (1st), WA (2nd), CL (3rd)	$\ln ML = 4.51 + 0.22 \ln WA + 0.14 \ln WL + 0.40 \ln CL$	0.92	$26.1_{(8,19)}$	$1.12*10^{-8}$

Table 2 Mean ± standard deviation values (in µm) for structures of the upper (UJ) and lower (LJ) jaws of paralarvae of *Chiroteuthis* cf. *veranyi* (N = 17 for both jaws), *Liocranchia reinhardti* (N = 16 for both jaws), and *Doryteuthis opalescens* (N = 27 and 28, respectively). ML = mantle length; HL = hood length; RL = rostrum length; JA = jaw amplitude; LWA = lateral wall aperture; UJL = upper jaw length; UJW = upper jaw width; WA = wing aperture; WL = wing length; WW = wing width; CL = crest length; LJW = lower jaw width.

Jaw	Structure	*Chiroteuthis* cf. *veranyi*	*Liocranchia reinhardti*	*Doryteuthis opalescens*
UJ	ML	6823.24 ± 1966.06	9917.19 ± 4902.14	4828.52 ± 1881.99
UJ	HL	119.06 ± 42.80	449.38 ± 268.84	212.48 ± 143.92
UJ	RL	8.98 ± 13.78	109.44 ± 84.30	49.19 ± 34.92
UJ	JA	45.65 ± 40.15	171.44 ± 80.82	102.07 ± 36.15
UJ	LWA	146.18 ± 22.65	244.5 ± 94.99	164.81 ± 41.60
UJ	UJL	307.94 ± 80.01	650.06 ± 279.82	389.33 ± 173.83
UJ	UJW	235.59 ± 43.00	432.38 ± 134.83	261.04 ± 80.91
LJ	ML	7271.47 ± 2548.89	9917.19 ± 4902.14	4751.07 ± 1845.04
LJ	HL	93.41 ± 38.26	240.63 ± 150.90	144.64 ± 71.19
LJ	RL	-3.51 ± 9.26	49.63 ± 47.05	0.22 ± 26.36
LJ	JA	82.12 ± 14.55	122.38 ± 65.84	93.11 ± 26.74
LJ	WL	143.65 ± 37.62	402.06 ± 184.95	161.82 ± 85.32
LJ	WW	37.24 ± 16.43	150.56 ± 80.08	55.93 ± 37.36
LJ	WA	160.24 ± 25.74	102.56 ± 44.08	139.71 ± 45.78
LJ	CL	149.94 ± 49.53	374.44 ± 205.95	217.54 ± 115.23
LJ	LJW	202.53 ± 41.46	299.94 ± 107.81	217.5 ± 76.09

Table 3 Results for ANOVA ($F_{(df1,df2)}$ and P) and TukeyHSD (P for each species pairwise comparison) tests for upper (UJ) and lower (LJ) jaw structures between paralarvae of *Chiroteuthis* cf. *veranyi* (N = 17 for both jaws), *Liocranchia reinhardti* (N = 16 for both jaws), and *Doryteuthis opalescens* (N = 27 and 28, respectively) (95% confidence interval). Significant differences between pairs of species on TukeyHSD test are indicated by underlined values. ML = mantle length; HL = hood length; RL = rostrum length; JA = jaw amplitude; LWA = lateral wall aperture; UJL = upper jaw length; UJW = upper jaw width; WA = wing aperture; WL = wing length; WW = wing width; CL = crest length; LJW = lower jaw width.

Jaw	Structure	$F_{(df1,df2)}$	P	*D. opalescens* and *C.* cf. *veranyi* (P)	*D. opalescens* and *L. reinhardti* (P)	*L. reinhardti* and *C.* cf. *veranyi* (P)
UJ	ML	$39.37_{(2,57)}$	$1.82*10^{-11}$	0.03	$1.8*10^{-6}$	0.02
UJ	HL	$15.37_{(2,57)}$	$4.58*10^{-6}$	0.11	$5.51*10^{-4}$	$3.5*10^{-6}$
UJ	RL	$39.75_{(2,57)}$	$1.55*10^{-11}$	$< 1.0*10^{-7}$	0.53	$< 1.0*10^{-7}$
UJ	JA	$37.54_{(2,57)}$	$3.97*10^{-11}$	$1.0*10^{-7}$	0.02	$< 1.0*10^{-7}$
UJ	LWA	$15.42_{(2,57)}$	$4.43*10^{-6}$	0.39	$1.04*10^{-4}$	$7.1*10^{-6}$
UJ	UJL	$13.99_{(2,57)}$	$1.14*10^{-5}$	0.36	$2.78*10^{-4}$	$1.52*10^{-5}$
UJ	UJW	$24.34_{(2,57)}$	$2.28*10^{-8}$	0.62	$4.0*10^{-7}$	$1.0*10^{-7}$
LJ	ML	$41.23_{(2,58)}$	$7.25*10^{-12}$	$7.46*10^{-3}$	$1.6*10^{-6}$	0.06
LJ	HL	$13.34_{(2,58)}$	$1.71*10^{-5}$	0.03	$7.26*10^{-3}$	$9.3*10^{-6}$
LJ	RL	$32.06_{(2,58)}$	$4.19*10^{-10}$	0.53	$< 1.0*10^{-7}$	$< 1.0*10^{-7}$
LJ	JA	$3.65_{(2,58)}$	0.03	0.51	0.15	0.03
LJ	WL	$30.73_{(2,58)}$	$7.96*10^{-10}$	0.93	$< 1.0*10^{-7}$	$< 1.0*10^{-7}$
LJ	WW	$28.37_{(2,58)}$	$2.55*10^{-9}$	0.16	$3.0*10^{-7}$	$< 1.0*10^{-7}$
LJ	WA	$10.21_{(2,58)}$	$1.59*10^{-4}$	0.21	$5.48*10^{-3}$	$1.22*10^{-4}$
LJ	CL	$14.00_{(2,58)}$	$1.09*10^{-5}$	0.08	$1.5*10^{-3}$	$7.3*10^{-6}$
LJ	LJW	$7.36_{(2,58)}$	$1.42*10^{-3}$	0.94	$3.21*10^{-3}$	$3.69*10^{-3}$