

# Body size and fin length as determinants in the geographic distribution of Loliginid squids

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## Research Article

**Keywords:** Squids, Macroecology, Phylogeny, Distribution, Dispersal capabilities, Loliginidae.

**Posted Date:** September 20th, 2022

**DOI:** <https://doi.org/10.21203/rs.3.rs-1926159/v1>

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**Version of Record:** A version of this preprint was published at Marine Biology on September 6th, 2023.  
See the published version at <https://doi.org/10.1007/s00227-023-04286-1>.

# Abstract

Macroecological studies have mainly focused on exploring the relationships between body size and geographic distribution on large scales, whether regional, continental or even global, and most of them have been conducted on terrestrial species. Few studies have been conducted on aquatic species, and even fewer have considered the importance of phylogeny in the observed patterns. Cephalopod molluscs are a good model to tackle these problems given that they have large geographic and bathymetric ranges, a wide range of body sizes, as well as diverse fin sizes and shapes. Here, we evaluate the relationships between body and fin size with the geographic distribution of 30 squid species of the family Loliginidae distributed worldwide. To test a macroecological hypothesis, we evaluated the phylogenetic signal and correlated evolution of the three traits to assess the role of phylogenetic relationships in squid distribution using a molecular phylogeny based on two mitochondrial and one nuclear gene. The analyses showed the existence of a relationship between body size and geographic distribution. Similarly, relative fin size showed a positive relationship with distribution. Phylogenetic signals were high for morphological traits (body and fin size), while it was low for distribution. The geographic distribution of loliginid squids evolved in relation to body size, where larger squids with large fins (e.g. genus *Sepioteuthis*) have wide distributions, while small-finned species (e.g. genus *Pickfordioteuthis*) have narrow distributions. This study opens the gates to explore such relationships in other squid families or other marine swimming animals.

## Introduction

Geographic distribution of species is determined by ecological and evolutionary factors, its dispersal abilities, and the environmental conditions (Brown et al. 1996). Locomotion mode can help species to migrate and disperse to colonize new habitats, and in consequence expand their geographic distributions. Species that evolved specialized anatomical structures to move large distances (i.e., wings, fins) have big geographical distributions (e.g., birds, bats, fishes) (Böhning-Gaese et al. 2006; Laube et al. 2013; Luo et al. 2019). Recently, Luo et al. (2019) demonstrated that bat species with bigger wings display larger distribution ranges than those with smaller wings, and that the size of geographic ranges was associated with wing aspect ratio. This study emphasizes the relationship between specialized anatomical structures and distributions, suggesting an important role of dispersal capacity in shaping species' geographic distributions (Luo et al. 2019). In the case of aquatic species that use fins as a means of locomotion (fishes and cephalopods) they could display distribution patterns similar to those reported for birds and bats (Laube et al. 2013; Luo et al. 2019).

Cephalopods are exclusively marine molluscs that includes nautilids, cuttlefishes, squids, and octopods, with around 860 species distributed in 50 families and 174 genera (Hoving et al. 2014; Luna et al. 2021), some species are large animals that can have wide geographical distributions (> 5,000 km) (Rosa et al. 2008 a, b; Ibáñez et al. 2019; Rosa et al. 2012, 2019), primarily inhabit the first 1,000 m depth and have daily vertical migrations (Young and Hirota 1990; Boyle and Rodhouse 2005). Those characteristics (wide

distribution, high dispersal and large body size) make cephalopods a good model to test biogeographic hypotheses.

Since all cephalopods have funnel and jet propulsion, the size and shape of fins could be determinant in their movement capabilities (Clarke 1988). Squids have nine different fin shapes that contribute to fast swimming and orientation control (following Clarke 1988; Boyle and Rodhouse 2005). These fins are muscular hydrostats with an intramuscular network of crossed connective tissue fibres that provide support for fin movements (Johnsen and Kier 1993). Loliginid squids display diverse morphologies, body sizes and a wide geographical distribution (Anderson 2000a; Jereb and Roper 2010). Loliginidae contains species which can reach a rather large size (at least 90 cm of mantle length, ML, in *Loligo forbesii* Steenstrup, 1856), along with dwarf species, like *Pickfordiateuthis* Voss, 1953, where males may mature at less than 1.4 cm ML. These benthopelagic squids have a pelagic larval stage, form schools, are active swimmers and pursuing predators (Nesis 1980). Loliginid squids have elongated flapping fins which produce large-amplitude waves for economical, gentle swimming and hovering as well as for controlling stability and aiding jet escape (Clarke 1988). By combining finning and jetting, cephalopods can generate different swimming gaits (Anderson and DeMont 2000; Stewart et al. 2010). The general loliginid evolutionary trend corresponds to the direction of morpho-physiological adaptation, pioneering new trails (Nesis 1980).

To understand the historical and ecological processes that influence the distributions of species is necessary to integrate comparative-quantitative biogeographic and phylogenetic studies (Brown et al. 1996). In this study we test predictions of macroecology based on data about the distribution, fin and body size of loliginid squids around the world. To make this possible, we assess distribution area, collecting body and fin size data, inferring their phylogenetic relationships to estimate phylogenetic correlation between traits. The goal of this study is to test whether geographic range size can be predicted by dispersal capacity, inferred from body and fin size, among loliginid within a phylogenetic comparative framework.

## Materials And Methods

### Database

Thirty loliginid squid species belonging to ten genera were considered in this study. We performed an exhaustive literature review to obtain data of squid body lengths (maximum mantle length, ML, in mm) as indicator of body size, fin length (FL, in mm) and geographical distribution (GD, km<sup>2</sup>). To avoid allometric effects, the fin length was transformed to FL/ML ratio (FLR, fin length ratio) (see supplementary material, Table S1). The distribution areas for all different species were estimated from the distribution maps reported in the literature (Jereb and Roper 2010). To accurately assess the extension of the reported distribution, these maps were georeferenced using the open-source GIS software QGIS 3.0.1 (QGIS Development Team 2018) with the plugin Georeferencer GDAL 3.1.9. Georeferencer assigns spatial information to a map picture, and each pixel is assigned a coordinate in geographic space (Fleet et al.

2012). From the georeferenced maps, the distribution area for each species was recreated as a polygon shapefile, and its area measured in square kilometres with the plugin Calculate Geometry 0.3.2. This database was combined with a new molecular phylogeny reconstructed with data from GenBank (Table S2).

## Phylogenetic analysis

We separately aligned the nucleotide sequences for each gene using Multiple Sequence Comparison by Log-Expectation (MUSCLE) with default parameters for gap insertion and gap extension (Edgar 2004), implemented in the MEGA X software (Kumar et al. 2018). Prior to the phylogenetic analysis, we identified the best-supported substitution model for each gene using jModelTest2 (Darriba et al. 2012) (Table S3). Once aligned, we used Mesquite v3.10 (Maddison and Maddison 2016) to concatenate our aligned sequences for each of the three genes (16S, COI, and RHO) into a single partitioned matrix, which allowed for a separate substitution model to be used for each gene (Table S2).

We estimated phylogenies for the partitioned dataset using Bayesian Inference with MrBayes v3.2 software (Ronquist et al. 2012). We performed Bayesian phylogenetic inference using 10,000,000 generations of four heated Markov Chain Monte Carlo (MCMC), sampling every 1,000 generations. We discarded the first 10% (or 1,000,000) of generations as burn-in, leaving us with a total of 9,001 trees sampled from the posterior probability distribution. From these trees, we computed a (50%) majority consensus tree. We also evaluated convergence to the posterior distribution and mixing of the MCMC using Tracer v1.6 (Rambaut et al. 2014). Effective Sample Size (ESS) > 200 were accepted. The trees were rooted using *Spirula spirula* Owen, 1836, *Ommastrephes bartramii* (Lesueur, 1821), and *Sthenoteuthis oualaniensis* (Lesson, 1830) as outgroups. To avoid including cryptic species or genetic lineages in some loliginid species (i.e., *Doryteuthis pleii*, *D. pealeii*, *Lolliguncula brevis* and *Sepioteuthis lessoniana*) in the phylogeny, we only use one of the lineages and its respective distribution.

For comparative purposes, all outgroup species (three tree tips, *S. spirula*, *O. bartramii*, and *S. oualaniensis*) were removed from the tree using the drop.tip function in “APE” package (Paradis et al. 2004) implemented in R v4.1.2 core (R Development core team 2022). The new phylogram was transformed into an ultrametric tree using the Grafen’s (1989) method. A heatmap was employed to explore the association between the standardized database and the phylogeny using the phylo.heatmap function in “Phytools” package (Revell 2012).

## Phylogenetic signal

The ultrametric tree was used to estimate the phylogenetic signal of each trait denoted as Pagel’s  $\lambda$  (Pagel 1999). Lambda ( $\lambda$ ) ranges between 0 and 1, and quantifies the amount of phylogenetic signal in the studied trait. When  $\lambda = 0$  means that the trait distribution (across species) is independent of the phylogeny, whereas a  $\lambda = 1$  indicates that the distribution of trait values fits as expected according to the Brownian motion model (Pagel 1999). The analyses were conducted using the phylosig function implemented in “Phytools”. The likelihood value of  $\lambda$  estimated for each trait was contrasted to the likelihood value of  $\lambda$  equal to 0 by means of a likelihood ratio test (LRT).

# Correlated evolution

Phylogenetic Generalized Least Squares models (PGLS; Pagel 1999) were used to establish the existence of a linear relationship between ML, FLR and GD. These models were performed using the corPagel function in “APE” package implemented in R. The correlation structure of PGLS was carried out under the assumption of Brownian motion model, multiplying the off-diagonal elements (i.e., the covariances) by  $\lambda$ .

## Results

### Biological data

The body length of the 30 loliginid species ranged from 2.2 cm in *Pickfordiateuthis pulchella* Voss, 1953 to 93.7 cm in *L. forbesii*, whereas fin length ratio ranged from 0.23 in *Alloteuthis africana* Adam, 1950 to 0.9 in *Sepioteuthis lessoniana* d’Orbigny, 1826 (Table S1). Geographic distribution ranged from 73,729 km<sup>2</sup> in *Lolliguncula argus* Brakoniecki and Roper, 1985 and up to 28,000,000 km<sup>2</sup> in *S. lessoniana* (Table S1).

### Phylogenetic signal

Squids ML and FLR were highly structured across the phylogeny in the heatmap (Fig. 1), with both traits exhibiting a high significant phylogenetic signal ( $\lambda > 0.75$ ,  $P < 0.001$ ; Table 1). These results show evidence that there is a concordance between loliginid phylogeny and both biological traits evaluated. Geographic distribution showed a low phylogenetic signal ( $\lambda = 0.022$ ,  $P > 0.5$ ; Table 1) and an absence of phylogenetic structure (Fig. 1).

Table 1  
Phylogenetic signal of each trait obtained with univariate analyses.

	Lambda ( $\lambda$ )	logLik $\lambda$	logLik $\lambda = 0$	P-value
ML	0.9529	-11.0877	-12.6303	0.0070
FLR	0.7610	19.2284	16.1182	0.0126
GD	0.0223	-25.3513	-25.3585	0.9048

## Correlated evolution

The largest loliginid squids and those with largest fins have wider distribution, evidencing a positive correlation between all traits (Fig. 2). The PGLS analysis showed a significant correlation between ML and FLR with GD ( $\beta > 0.80$ , Table 2, Fig. 2), whereas the best predictor of geographic distribution of loliginid squids was FLR ( $\beta = 1.92$ , Table 2, Fig. 2B). The allometric correction on traits resulted in a positive relationship between FLR and ML ( $\beta = 1.57$ ,  $P < 0.001$ , Fig. 3), indicating FLR increased with squid’s body sizes evidencing that is impossible to avoid the body length scaling.

Table 2  
Parameters of the relationship among mantle length (ML), fins length ratio (FLR), and geographic distribution (GD) of loliginid squids obtained by phylogenetic generalized least squares (PGLS) analyses.

	GD ~ ML	GD ~ FLR
$\lambda$	0.231	0.035
logLik	-20.4097	-22.0705
$\alpha$	4.0303	4.9668
$\beta$	0.8989	1.9245
SE	0.2312	0.6571
t-value	3.8865	2.9285
<i>P</i> -value	< 0.001	0.0067

## Discussion

Geographic range size—the extent of a species occurrence—is a basic biogeographic variable influenced by several intrinsic and extrinsic factors (Brown et al. 1996; Gaston 2003). In the case of Loliginid species, we found that larger species with larger fin sizes would have a wider distribution range, similar to the positive correlation between wings and distribution of birds and bats (Böhning-Gaese et al. 2006; Laube et al. 2013; Luo et al. 2019). This macroecological relationships suggests exploring these patterns in other squid families or other marine swimming animals (e.g., fishes).

## Body size and distribution

Our results show that loliginid squids with larger body size exhibits higher geographic distribution and small species a restricted distribution like marine fishes (Hernández et al. 2013). However, for hundreds of millions of years cephalopods roamed the world's oceans as jet-propelled masters of the pelagic world, until fishes, using highly efficient undulatory locomotion, deprived them from many nektonic habitats (Hoar et al. 1991). According to Nesis (1980), the evolution of squids, as Loliginidae, has been marked by a strong competition with fish, and determined by the prevalence of competition between squid species during their evolution. In fact, their biology, distribution, and geographic variation come determined by direct competition between species, occupying different ecologic habitats (depth, thermal preferences) as well as having inverse circadian levels of activity (Martins and Juanicó 2018). Indeed, the directional jet propulsion of the cephalopods provide acceleration and manoeuvrability better than many fishes (Foyle and O'Dor 1988), and, combined with lift production by the fins may make dynamic lift more efficient for

squids (Hoar et al. 1991). The relationship between body, fin and geographical range size in our results suggests a role of dispersal capacity in shaping species' geographic distributions. Without a geographical or ecological barrier to prevent it, larger squid will have a greater dispersal capacity and, thus, reach a wider range of distribution.

Some species falling above the regression line (Fig. 2) have bigger distribution ranges than its body size predicted. This pattern is associated to paralarval dispersion since eggs are deposited on the seabed or on sessile organisms (kelps, corals, Carrasco et al. 2021). Species falling below to regression line have smaller spatial distribution than predicted by its body size, indicating a reduction of distribution or a scarce knowledge of its distribution.

The geographic distribution (i.e., area) does not show significant phylogenetic signal throughout the family. This is contrary to the stated by other authors (Brakoniecki 1986; Anderson 2000a, b; Ulloa et al. 2017), which postulated that geographically close species share common ancestors. Which hypothesis is more accurate should be tested by analysing a larger sample size, such as the total of the 47 currently accepted loliginid species (WoRMS 2022). The geographic distribution of loliginids evolved in relation to body size, where larger squids with large fins (*Sepioteuthis* Blainville, 1824) have wide distributions, while small species with small fins (*Pickfordioteuthis*, *Afrololigo*) have narrow distributions (Fig. 1) – although *P. pulchella* has a very broad distribution through the tropical western Atlantic Ocean (Jereb and Roper 2010). It was known that a positive relationship between geographic range size and body size exists (Diniz-Filho and Tôrres 2002; Hernández et al. 2013), which is consistent with the relationships between mantle length and geographic distribution in our results (Fig. 2). However, the existence of a great variation in the sizes of geographic ranges of small species is a common pattern in macroecology (Brown 1995) and related to dispersal capacity in some cases of their early life stages (i.e., larvae) (Brown et al. 1996; Villanueva et al. 1996). In this case, geographical distribution of loliginid squids is influenced by their environment and life history (Sales et al 2017; Costa et al 2021). One of the most important of these is the dispersion capacity. For some American Loliginid species of the *Doryteuthis* and *Lolliguncula* genera, the Amazon plume Barrier (Floeter et al. 2008) do not rampart the dispersion of *D. pleii*, *D. pealeii* and *L. brevis* to be found above the major influence area of the plume (between Pará and Amapá states, and North Coast of Brazil and Isla Margarita (Venezuela), Muller-Karger et al. 1988; Hoorn et al. 2010), that strongly reduces salinity. The latter can act like a barrier for both adults and palalarvae that show high mortality in low salinity environments (Hanlon and Messenger 1996; Hanlon 1998; Boyle and Rodhouse 2005) but these three species can simply disperse above the plume area of influences showing the considerable capacity of dispersion of Loliginid squids (Boyle and Rodhouse 2005; Jereb and Roper 2010).

Size and shape have important implications for the hydrodynamics of marine organisms (DeMont and Hokkanen 1992). The fact that geographically close species do not share common ancestors may be determined by the biology and dispersal ability of each species; indeed, the high mobility of Loliginidae adults (Boyle and Rodhouse 2005) cause that its dispersion will be bigger. A notable case is that of both neritic species of the genera *Loligo* Lamarck, 1789, that have a high dispersal ability, and an evident

difference between the maximum ML of their males, which it could be one of the reasons for habitat choice [*L. forbesii* (maximum ML of 93.7 cm in males; 46.2 cm in females) and *Loligo vulgaris* Lamarck, 1798 (ML of 64 cm in males; 48,5 cm in females)]; Jereb and Roper 2010). Another contrast between these species is the spatio-temporal variability of spawning and nursery grounds where their life cycle takes place (Laptikhovsky et al. 2022), which could benefit their capacity of scattering too.

There are exceptions, such as *L. argus*, a coastal species characterized by its small size at maturity (Jereb and Roper 2010), which would decrease its potential final size. This species reaches the less area of all the studied loliginid species (73.7 km<sup>2</sup>). Embryos hatch into planktonic stage and live for some time before they grow larger and take up a benthic existence as adults (Hochberg and Camacho-García 2009). A similar case occurs in the small species that inhabits sandy-mud bottoms *Afrololigo mercatoris* Adam, 1941 (ML of 3.5 cm in males; 5 cm in females; Jereb and Roper 2010), which shares many morphological traits with *Lolliguncula* Steenstrup, 1881 (Jereb and Roper 2010), such as the small size. The medium-sized shelf species *Uroteuthis* (P.) *edulis* (Hoyle, 1885) (maximum ML of 50.2 cm in males; 41 cm in females; Jereb and Roper 2010) exhibits a big fin (in adults, it can reach 70% ML in length, 60% ML in width), as well as its congener *Uroteuthis* (P.) *chinensis* (Gray, 1849) (maximum ML of 49 cm in males; 31 cm in females; Jereb and Roper 2010), with a fin spreading to two-thirds of the ML. However, both *Uroteuthis* have lesser extensive range of distribution that it would be expected by their size.

Marine mollusc species that do not have a planktonic larval phase in their life cycle tend to have smaller ranges of size than do species with more readily dispersed planktotrophic larvae (Brown et al. 1996; Ibáñez et al. 2018). In fact, in some Neogastropoda snails, wide distributions, free gene flow, and resistance to isolation gave planktonic species an evolutionary stability that resulted in greater species longevity (Hansen 1980). Loliginids have a pelagic paralarval stage in which they spend two to three months as zooplankton (García-Mayoral et al. 2020), during which time they disperse but remain on the continental shelf by controlling their vertical position (Roura et al. 2016, 2019). Therefore, they will tend to have big ranges of size, and hence, and geographical distribution, which is consistent with our results. In fact, the high dispersal rates of the most squid species, due to lengthy planktonic paralarval stages and highly migratory adult stages, lead to predict panmixia (genetic homogeneity) of squid populations across large geographical areas (Shaw et al. 2010). However, many loliginid squids show structure population at large scales (Brierley et al. 1995; Shaw et al. 1999; Herke and Foltz 2002; Aoki et al. 2008; Ibáñez et al. 2012).

Other important factor for the dispersal capacity of the loliginids is the speed they can achieve in swimming and their manoeuvrability, combining finning and jetting to generate different swimming gaits (Anderson and DeMont 2000; Stewart et al. 2010). For instance, there are differences between the locomotive repertoire and a high degree of manoeuvrability enabled by fin propulsion of *Lolliguncula brevis* (Blainville, 1823) (Bartol et al. 2001) than the moderate-high speeds relying heavily on jetting for propulsion of the ommastrephid *Illex illecebrosus* (Lesueur, 1821) swims at (O'Dor et al. 1995). In the first species (maximum ML of 8.5 cm in males; 12 cm in females; Jereb and Roper 2010), their swimming gaits could help them to achieve the same distributional range than other bigger loliginids. The high diel



vertical migration behavioural flexibility expressed by *L. forbesii*, could be very advantageous in terms of energy conservation, prey capture, and predator avoidance (Cones et al. 2022), which would translate into greater evolutionary success and, consequently, a greater dispersal capacity than expected for its size.

## Fins length and distribution

FLR exhibits a high significant phylogenetic signal, showing the existing concordance between the fin length and loliginid phylogeny. The shape of the fins changes during ontogenetic growth, and nearly all hatching squid have fins proportionally smaller than those of adults. This change in relative size may also reflect a change on the use of the fins similar to the different usages of the variously shaped adult fins (Hoar et al. 1991). The shape of the lateral fins of cephalopods varies in accordance with the size of the animal and the way of life of the animal (Packard 1972), being hydrodynamic constraints the major determinants of fin shape (Daniel 1988). For instance, oceanic squid (such as the ommastrephids) have small, triangular fins that appear to function mainly as rudders, more useful at the lower speeds of a coastal environment, whereas the coastal loliginid squids have large, rhomboidal fins useful for propulsion or “soaring” in currents, forcing these animals to depend more on the jet-propulsion system (O’Dor et al. 1991, 1995; Hoar et al. 1991). For species such as from *Uroteuthis* genus that do not use ammonia for buoyancy, fins are an efficient way of maintaining position in the water column (Wells 1990). As growth occurs, and the animal moves from a viscosity-dominant to an inertia-dominant system, development of the fin structure becomes important, having shape further implications for friction and pressure drag on animals during movement (Moltschaniwskyj 1995).

*Sepioteuthis lessoniana* is a species widely distributed throughout the Indo-Pacific and Mediterranean regions being the species with the widest range of distribution. It has been proposed as a complex of cryptic species (Okutani 1984, 2005; Segawa et al. 1993; Cheng et al. 2005). The genus has very large and distinctive fin, broadly oval in outline and with a fin length over 90% up to nearly 100% of ML (Jereb and Roper 2010), very different from other loliginids. Conversely, *Sepioteuthis australis* Quoy and Gaimard, 1832, is distributed in the southwestern Pacific Ocean and is differentiated from *S. lessoniana* by the angular lateral margins of fins (Jereb and Roper 2010). The distant geographic distribution of both species could clarify this contrasting phylogenetic footprint. On the other hand, the smallest FLR and reduced distribution among loliginids correspond to *A. africana* and *L. argus*. The small coastal species *A. africana* (maximum ML of 20.5 cm in males; 17,5 in females; Jereb and Roper 2010) has a remarked sexual dimorphism displaying the characteristic extremely long and spike-like tail in males (73% of the dorsal ML in adults) as secondary sexual trait, which could break the average deviation from FLR and fin shape, since this feature is not a trend in the family.

In this comparative study, we evaluated the potential effects of body size and fins of squids as predictors of its geographical distribution under a phylogenetic approach. This approach has been scarcely used in macroecological studies on marine animals, and particularly, the assessment of phylogenetic signal on geographic distribution (i.e., Hernández et al. 2013; Ulloa et al. 2017). In this sense, our research is among the first studies correctly addressing trait comparisons for marine animals, suggesting that further research should incorporate this approach in macroecological studies. New approaches to the knowledge

of the distributional range of mobile species, such as the bio-logging tags (Flaspohler et al. 2019; Cones et al. 2022) could help in an accurate determination of the real extent of the species, as well as their biological activity and behavioural patterns.

## Declarations

### Compliance with Ethical Standards

The authors declare that they have no conflict of interest. Ethical review and approval were not required for this study because this work does not contain any experimental studies with live animals. Biological, distributional data and sequences were taken from open sources (i.e., GenBank, FAO books).

## Acknowledgment

We would like to thank Francisco Rocha for the comments on the initial stages of the manuscript. This work was partially funded by the grant REG UNAB 04-2020 to C.M.I..

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## Figures



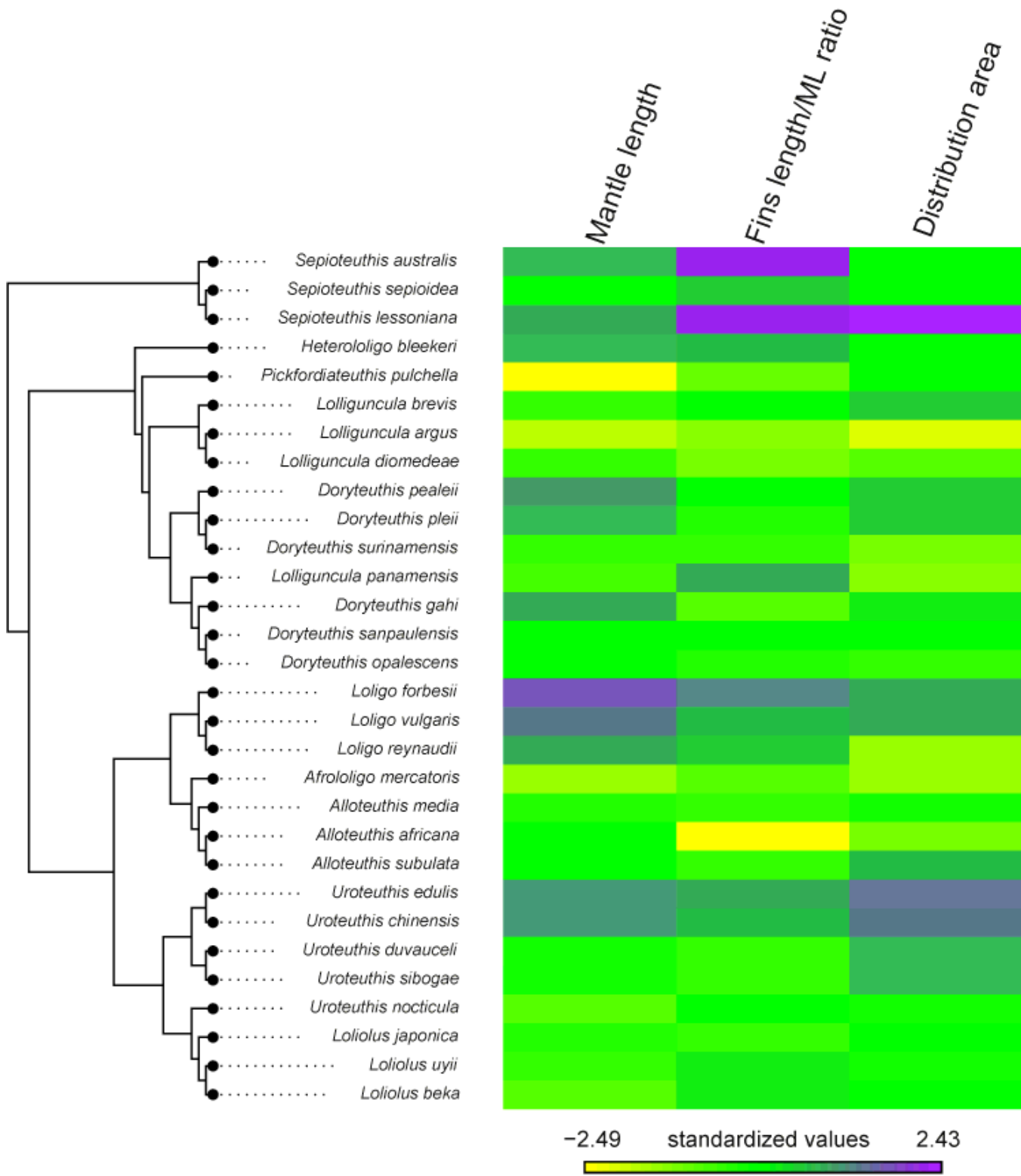
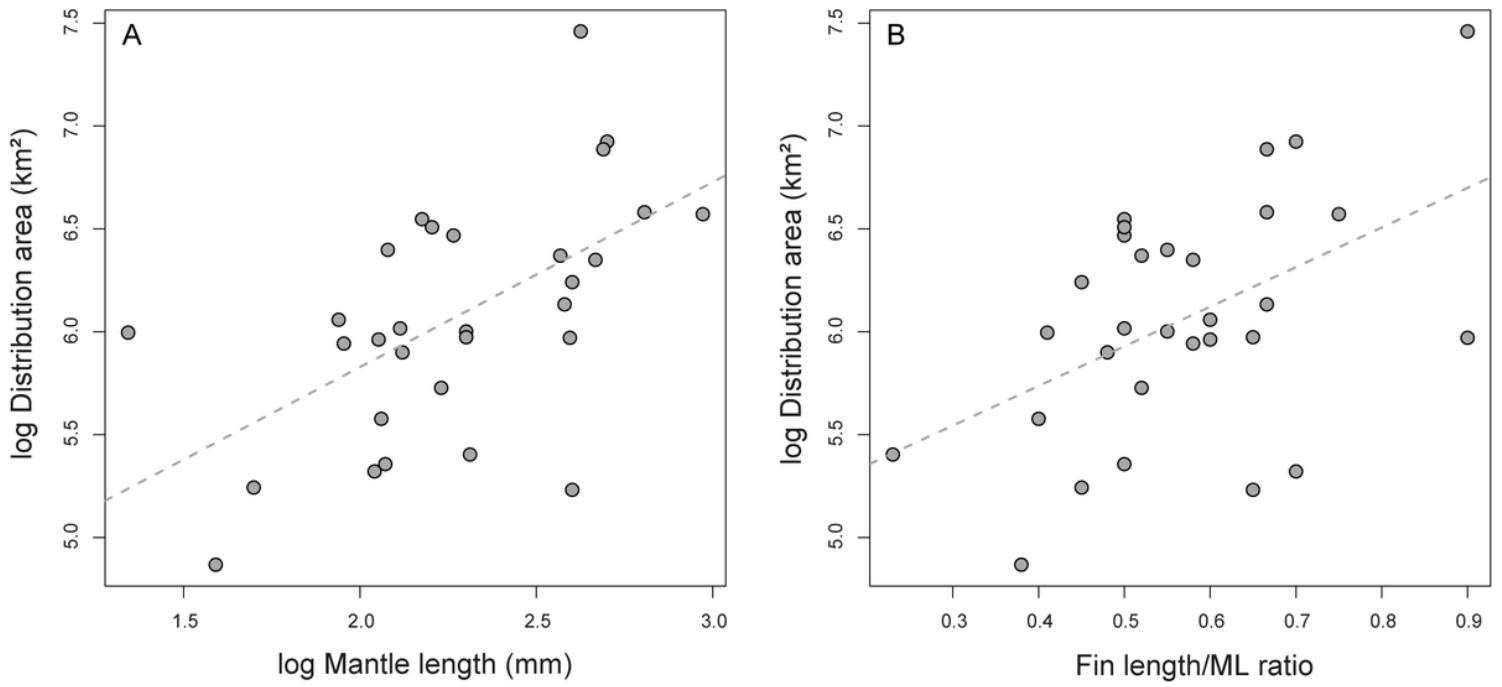


Figure 1

Phylogenetic heatmap tree of loliginid squid traits (mantle length, fins length ratio, and geographic distribution).



**Figure 2**

Plots with the relationships between biological and distributional traits of loliginid squids, where (A) mantle length / geographic distribution, (B) fin length ratio / geographic distribution. Dashed lines represent regressions from PGLS.

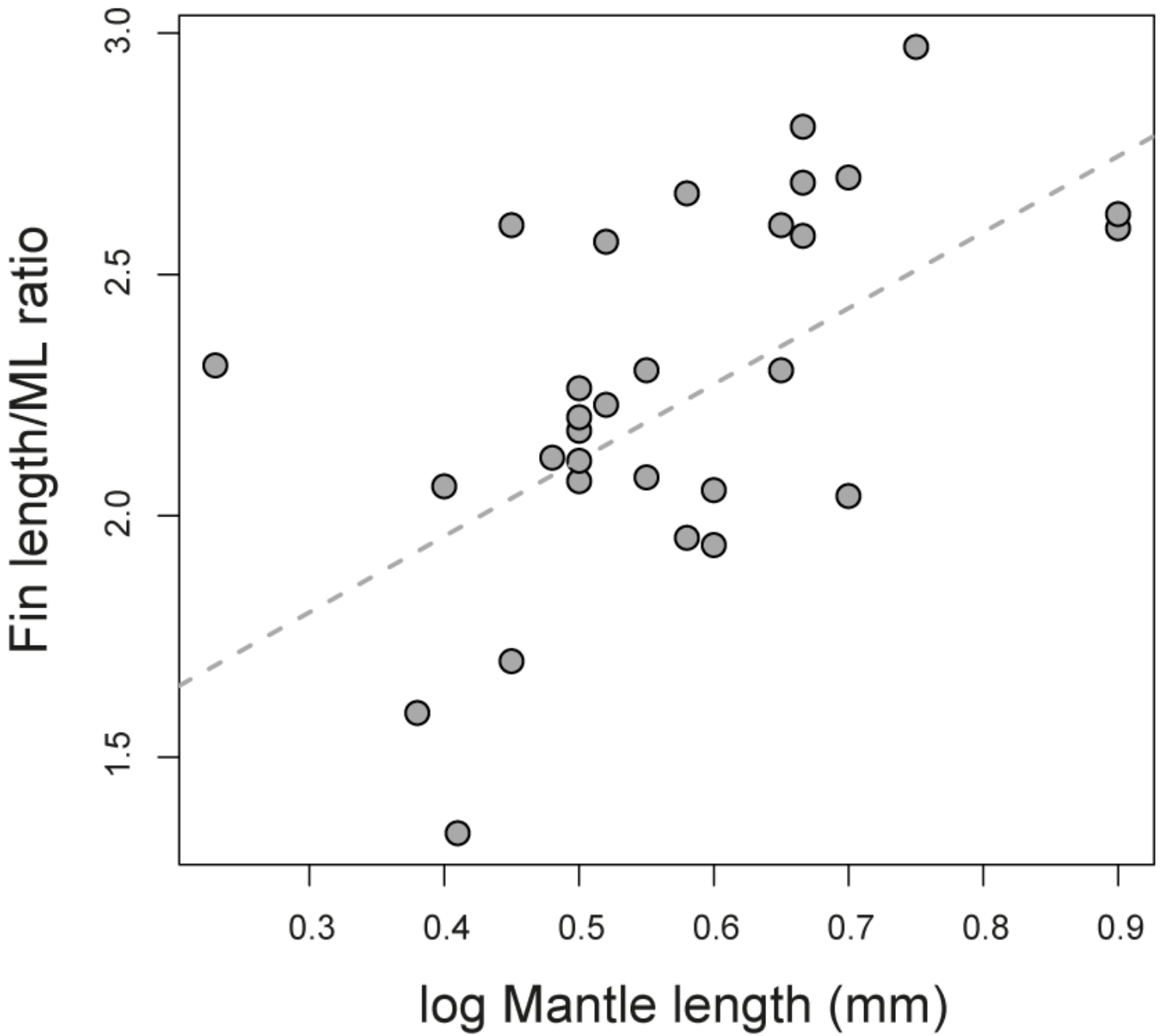


Figure 3

Relationships between body size and fin length / mantle length ratio of loliginid squids. Dashed lines represent regressions from PGLS.

## Supplementary Files

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