Coleoid Cephalopods Demonstrate Asocial Path to the Evolution of Big Brains

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Abstract
Coleoid cephalopods have large brains, complex nervous systems and show signs of intelligent behavior comparable to birds, cetaceans, and primates. However, contrasting with many large brained vertebrates, many cephalopods live largely solitary, semelparous, and short lives, leaving little to no opportunity for parental care, complex group dynamics, or social learning. Here, we introduce and analyze a comprehensive database of brain size, ecology, behavior, sociality, and life history of 79 diverse species of octopus, squid, and cuttlefish, including an updated phylogeny using Bayesian multilevel linear regression models. In a set of pre-registered statistical models, we find a large effect of habitat, suggesting ecology as a primary selection pressure on brain size in cephalopods. We also find some evidence of a positive relationship between brain size and number of predator groups, and no relationship between brain size and sociality. Taken together, these results are inconsistent with social explanations for brain evolution but consistent with ecological explanations, including the "Asocial Brain Hypothesis"- a regime of predictions from the "Cultural Brain Hypothesis"- and emphasize how these animals, which diverged from humans and other vertebrates over 500 million years ago, offer an insightful comparative study of the evolution of large brains.

Introduction
The evolution of large brains across the animal kingdom has been a subject of extensive research, with various social, behavioral, developmental, and ecological factors being proposed as key drivers of this energetically costly adaptation[1–4]. Comparative studies have identified a range of predictors for larger brains, including group size, social structure, sexual competition, parental care, length of the juvenile period, predation pressures, diet, locomotion, and sensory capabilities[5–9]. Among these, the role of sociality has gained significant attention. Initial work by Jolly[10] and Humphrey[11] argued for social complexity as a driver for intelligence among primates. The social brain hypothesis, developed to explain the evolution of large brains in primates[12], predicts the evolution of larger brains to cope with the complex demands of social group living, such as cooperation, deception, and competition[13–15], as well as pairbonding and social cohesion[16,17]. In addition to primates, it has been examined with mixed empirical success among various taxa including other mammals; e.g. carnivorans[18], rodents[19], bats[20], and cetaceans[21] , as well as birds[16,22,23], non-avian reptiles[24], fishes[25], and insects[26,27]. Other researchers have emphasized the importance of ecological complexity in driving brain size, focusing on the cognitive abilities required for innovation, problem-solving and foraging for difficult-to-extract or high-energy foods[28–30]. Others again have emphasized the role of life span, life-history and development[31–33].

Muthukrishna and colleagues attempted to reconcile these disparate and sometimes contradictory[5,23,34] results under a unified formal theoretical framework, the "Cultural Brain

Hypothesis" (CBH)[35]. The CBH, following previous work on cultural intelligence[11,36,37] shifted the focus from sociality to learning, both socially and asocially, and development with a particular focus on ecological and social constraints and payoffs to information. Three sets of predictions were derived from this model, one of which – a social learning path to larger brains – has been tested with primates[35] and cetaceans[21]. The second set of predictions, the *Cumulative* Cultural Brain Hypothesis, revealed a narrow set of parameters within the social learning path that would lead to an autocatalytic takeoff consistent with the human pathway characterized by an ever-increasing reliance on culture and technology (see also[38]).

The model also identified a third set of predictions for brain size in taxa that primarily rely on asocial learning (e.g., through individual trial-and-error). According to the CBH, animals on this asocial learning path to larger brains are characterized, among other things, by a weak or non-existent relationship between sociality (e.g., group size), length of the juvenile period, and brain size. While species relying on social learning delay reproduction to allow more time to learn from their large groups, species on the asocial learning path have a reduced juvenile period so they can move quickly from exploring to exploiting information[39]. Muthukrishna et al. argue that – possibly due to biases against publishing null results – there is a dearth of data on non-socially learning species, making these predictions difficult to test. We refer to this as yet untested set of predictions as the "Asocial Brain Hypothesis" (ABH). One well-studied, primarily asocial animal group in particular, namely the large-brained coleoid cephalopods, offer a unique opportunity to study this regime.

With a last common ancestor with humans and other vertebrates over 500 million years ago, cephalopods not only have flexible bodies, but also flexible cognition and behavior. For instance, many species of cephalopods exhibit a variety of foraging and predator-avoidance strategies[40]. These strategies, such as camouflage, navigation, mimicry, and tool use can be flexibly adjusted to nearby species or other contextual cues[41,42]. Although they do not display the cohesion and complex sociality of many mammalian and bird species, communicative body patterns are used widely across the squid and cuttlefish in mating contexts, where aggressive visual signaling as well as tactical deception have been observed in a range of species[43–45]. Many species, especially the well-studied *Octopus vulgaris*, display cognitive abilities such as tool use, navigation and problem solving as well as many types of learning[46]. Playful behavior, an otherwise rare occurrence in the animal kingdom, has also been observed in some octopuses[47].

Cephalopods, then, represent an independent evolutionary origin of intelligence from that of the vertebrate animals we often view as possessing advanced cognition, such as primates, cetaceans, and birds. At the same time, cephalopods are generally short-lived and asocial. Many are cannibalistic, a barrier to social tolerance let alone sociality[48]. Cephalopods also exhibit little to no parental care or pair-bonding, often dying after first reproduction[49–51]. As these characteristics run counter to established theory and empirical findings from other, more social, vertebrate taxa, cephalopods are a promising animal group on which to evaluate prominent hypotheses on the evolutionary drivers of brain size[52–54].

The most comprehensive comparative study on cephalopod brain size to date was published as part of a PhD dissertation by Borelli[55] and in a subsequent journal article by Ponte and colleagues[56]. While an ambitious and useful first step, this effort had limitations with regards to broader research efforts on comparative brain evolution. First, Borrelli's dataset expresses brain size in relative terms (specifically, the size of each brain lobe is computed as a proportion to the whole central nervous system) and does not include absolute brain and body

size measurements. Second, Borrelli's dataset also does not include social, behavioral, or life-history variables necessary for directly evaluating predictions of evolutionary hypotheses for comparative brain size and cognition. Third, due to the fragmented nature of available cephalopod phylogenies, Ponte et al.[56] were forced to discard data on many species when running phylogenetically-controlled analyses. Fourth, upon reviewing Borelli's primary brain data sources[51,57,58] and their subsequent use in the literature, we found inconsistencies that ultimately called for a careful, systematic re-evaluation (refer to Supplementary Information for details). Finally, considerable advances in empirical work on cephalopods, including additional brain data measurements, have been made since Borelli's pioneering data collection.

The present study overcomes these limitations. We systematically surveyed the cephalopod literature to identify and capture a wide variety of qualitative and quantitative data on extant coleoid cephalopod species' brain and body size, physiology, ecology, life-history, sociality and behavior. Through combining previously published phylogenetic analyses and additional sequence data on GenBank, we also compiled a phylogeny that covers those species for which comparable adult brain size data are available ($N = 79$). We built this dataset with two main goals[39]: (1) to assess key hypotheses on the evolutionary drivers of brain size in cephalopods, including the ABH and (2) more generally, to move toward a theoretical reconciliation of empirical findings from comparative brain size studies in other animal groups. Drawing on these predictions as well as previous brain evolution literature, here we empirically assess whether measures of ecology, age at sexual maturity (i.e., length of juvenile period), sociality, and behavioral complexity predict brain size in coleoid cephalopods.

Results and Discussion

The Asocial Brain Hypothesis predictions from Bendizen et al.[35] were pre-registered as applicable to cephalopods (https://osf.io/nbwsx). Here we present the key results for each pre-registered set of hypotheses. All analyses are Bayesian multilevel linear regression models with total central nervous system (CNS) volume as the outcome variable with missing covariates imputed during model fitting. Each model also includes as a predictor dorsal mantle length (ML) as a standard measure of cephalopod body size[59]. All continuous variables are logged and standardized (mean 0, standard deviation of 1) and all models incorporate phylogenetic relationships as a correlation matrix to account for evolutionary relatedness between species; for further details on model specification and variable operationalization, see the Methods section. All analysis code and data are openly available.

For each model, we report the point estimate for the mean of the posterior distribution and the lower and upper bounds of the 95% Credibility Interval (CI) and the result plots report marginal posterior predictions with covariates held at their mean. A headline summary of the results for the main variables is presented in Table 1. As mantle length is a reliably large and positive predictor of brain size (a posterior mean point estimate of ~0.75 across models on a logged and standardized scale) with a known biological cause, for ease of interpretation, we interpret the coefficients of our predictors relative to this estimate as this is plausibly the largest effect size we could observe (i.e., body size should be the strongest predictor of brain size).

Table 1

Hypothesis/Variable	**Strength of relationship relative to ML:brain relationship**	**Sign of relationship**	**Results consistent with ABH**	**Strength of evidence***
Depth	<⅓ (maximum depth); ¼ (minimum depth)	negative	yes	medium
Benthic (vs. pelagic) habitat	~⅔	positive	yes	strong
Dietary breadth	~0	-	no	weak
Number of predator groups	<¼ (conditional on habitat); otherwise 0	positive (conditional on habitat)	yes (conditional on habitat); otherwise no	weak
Sociality	~¼	negative	yes	medium
Age of sexual maturity	<¼ (minimum); <¼ (mean); ~⅓ (maximum)	negative (minimum); positive (mean and max)	yes	weak
Foraging behaviors repertoire	<¼	negative	no	weak
Defensive behaviors repertoire	~0	-	no	weak
Cognitive repertoire	~0	-	no	weak

*Informal strength of evidence assessment based on amount of missing data, source data quality, effect size, CI ranges, and accuracy of variable definitions, as discussed in the main text. "Minimum", "maximum" and "mean" refers to the minimum, maximum and mean of minimum and maximum recorded values.

Ecological complexity

For asocial learning species such as cephalopods, the ABH predicts a positive relationship between brain size and richer ecologies[35] This prediction emerges in the model because richer ecologies with more calories can support larger brains for both social and asocial learners. Additionally, this relationship is expected to be reinforced by a greater behavioral repertoire leading to more access to calories consistent with ecological explanations for brain evolution. In our statistical models, ecological complexity was operationalized as: dietary breadth, measured through the number of taxonomic categories consumed (e.g. crustaceans, gastropods); habitat type; number of predators, also measured through the number of

taxonomic categories (e.g. other cephalopods, bony fishes); and depth in meters and broad categories (shallow, deep, ontogenetic or daily migration).

Depth

Minimum recorded depth had a negative effect (-0.14 [-0.27, -0.01]). The interaction with habitat was mostly negative for pelagic species (-0.13 [-0.30, 0.02] and did not appear to be present within benthic species (-0.03 [-0.32, 0.25]) (Fig. 1a). Maximum recorded depth also had a negative effect (-0.22 [-0.38, -0.05]). The interaction with habitat, the effect was mostly negative within pelagic species (-0.76 [-1.19, -0.31]) and positive among benthic species (0.63 [0.15, 1.10]) (Fig. 1a). Considering depth as a 4-factor categorical variable, categorizing species into shallow water, daily vertical migration, ontogenetic migration (usually descending as they grow from paralarvae/juveniles to adults), and deep sea also indicated lower CNS for ontogenetically migrating species (-0.85 [-1.346, -0.24]) and deep-sea species (-0.70 [-1.21, -0.20]) (Figure S1).

Habitat

A three-category measure of habitat (pelagic, benthic, and near bottom/demersal) showed a positive effect for near bottom/demersal habitat species (0.64 [0.09, 1.20]) and for benthic species (0.54 [-0.02, 1.09]) (Supplementary Fig. 1). The near bottom/demersal is a researcher classification. Considering habitat as a binary variable, with the near bottom/demersal species coded as benthic, the effect of benthic habitats on CNS was still positive (0.58 [0.08, 1.07]).

Latitude

Latitude was measured through minimum and maximum recorded ranges of species in degrees.

Latitude range had a slightly negative effect (-0.16 [-0.32, -0.01]). Mean latitude did not indicate any effect (-0.01 [-0.15, 0.12]).

Dietary breadth and predation pressure

Diet breadth was not associated with a larger brain size (0.02 [-0.20, 0.25]). The interaction with habitat, the estimates were weakly negative for pelagic (-0.09 [-0.46, 0.31]) and weakly positive for benthic (0.13 [-0.27, 0.52]). Number of predator taxa was weakly positive (0.08 [-0.11, 0.27]). When considered in interaction with habitat, this effect was close to 0 among pelagic species (0.04 [-0.18, 0.25]) and somewhat positive among benthic species (0.24 [-0.10, 0.54]). (Figure 1b.)

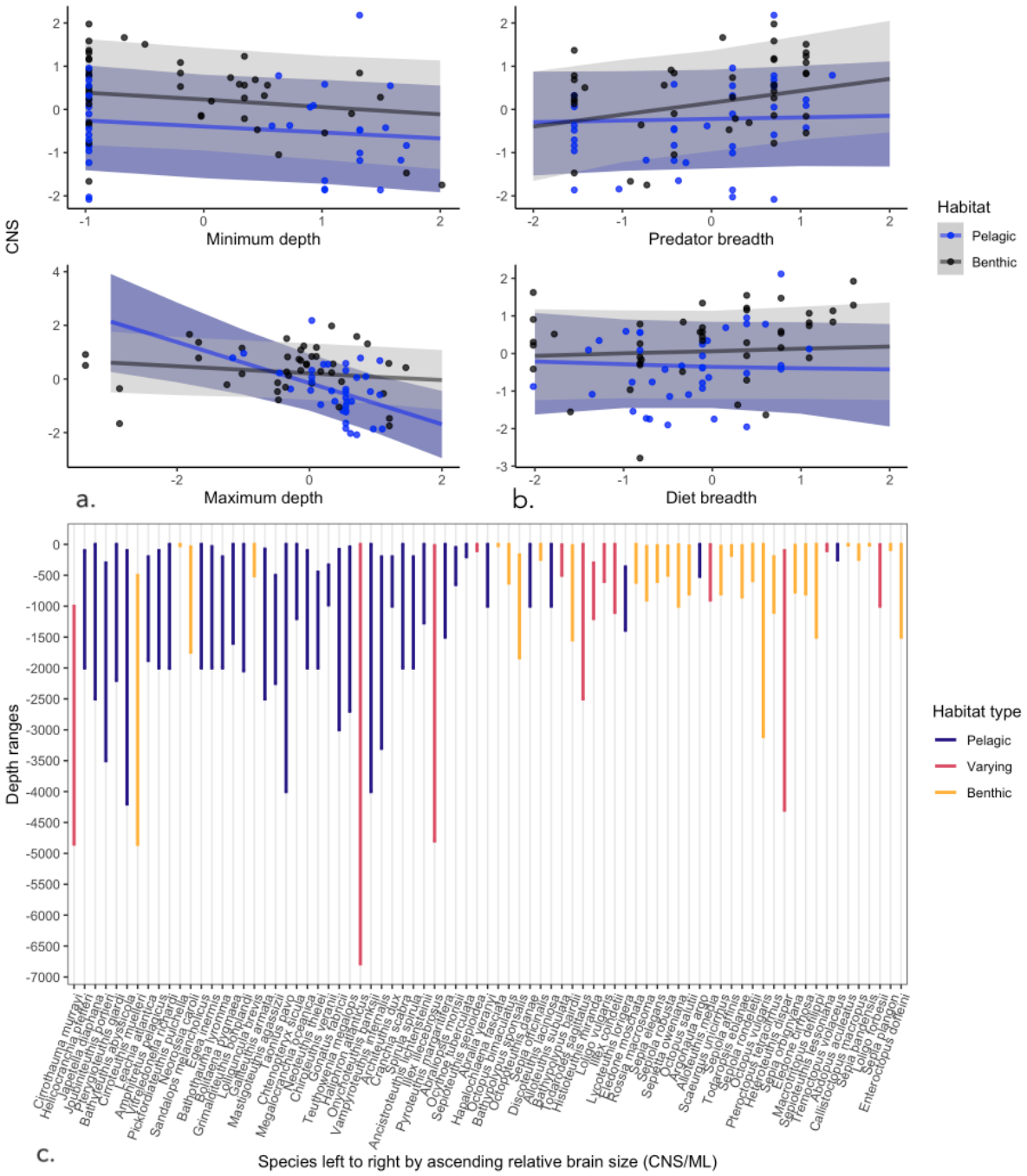

Figure 1. a) Posterior estimates for CNS predicted by minimum (top) and maximum (bottom) recorded depth among pelagic (blue) and benthic (grey) species. Lines indicate posterior medians and shaded areas highest density continuous intervals. CNS and depth are logged and standardized. b) Posterior estimates for CNS predicted by predator breadth (top) and dietary breadth (bottom). CNS and depth, predator breadth, and diet breadth are logged and standardized. c) Depth ranges for species, ordered left to right by ascending brain size (CNS/ML) and colored by habitat type.

Overall, whether a species occupied a primarily benthic or pelagic habitat appeared to be a reliable predictor of brain size with a posterior mean estimate of approximately 0.5 for benthic habitats in focal models, although with relatively wide CIs. For comparison, the point estimate for mantle length - a strong predictor of brain size - is approximately 0.75 across models (Table 2). The habitat variable is complete in our dataset and it is generally clear from the scientific literature whether species primarily live in the benthos or open water column,

although there is ambiguity with a few species that may primarily live and/or hunt in different habitats and have not been sufficiently observed (e.g. the bobtail squid *Heteroteuthis dispar* and some loliginid squids like *Loligo vulgaris* and *Loligo forbesii*). That said, the effects in our 3-category habitat model taking into account these edge cases and the consistent positive effect of benthic habitat across models indicate that benthic and pelagic lifestyles have been a selection pressure for brain size in cephalopods.

The effect of depth appeared to overall be negative, with maximum, minimum, and mean depths all having primarily negative posterior distributions. Although this is generally consistent with our predictions (assuming that shallow habitats tend to be more complex than deep-sea ones), depth measures in our dataset are somewhat imprecise given that many species have wide and/or variable ranges or engage in vertical migration, and the potential biases in measurement methods (e.g. different capture methods in fisheries studies). However, the categorical measure of deep-sea lifestyles and ontogenetic migration to the depths also showed lower estimates of brain size. Overall, further research on specific environmental aspects of different depths, as well how variables like predation pressures and prey availability differ for cephalopod species inhabiting benthic or pelagic habitats[60] will likely shed more light on ecological selection pressures on brain size.

Diet breadth in isolation was not a clear predictor of brain size with an estimate centered evenly around 0. The interaction with habitat, the estimate was positive for benthic species with an effect size around ⅕ that of brain-body size (although with relatively wide CIs). Diet breadth is a sparse variable from indirect measurement methods (sum of taxonomic categories of prey species). With more systematically collected observational data, the relative effects of both diet breadth and type on brain size could be examined with more precision. The effect of predator breadth was more reliably positive with the bulk of the posterior distribution being positive, which was also stronger for the interaction with habitat. Like diet and number of defensive and foraging behaviors, this is a variable dependent on observations in the wild or data from stomach content of predator species, so further field research will provide a more accurate assessment of predation pressure across species and how this variation affects brain sizes.

The results of the analyses conducted with the first version of habitat codes are consistent with the predictions of the ABH of selection for larger brains in more complex habitats. However, this is complicated by some species displaying elements of a pelagic lifestyle in addition to interacting with the benthos. While benthic habitats can be considered more heterogeneous than pelagic ones with greater species richness, these measures are highly scale-dependent[61,62]. Defining either habitat as more complex is also dependent on factors such as latitude, depth, substrate, and specific organismal lifestyles (e.g. diel vertical migration). Additionally, much remains to be discovered about organisms inhabiting the deep sea, open ocean, and other environments[63,64]. Depth range as a potential proxies for ecological complexity did not positively predict larger brains in our analyses (it did show a negative effect but this was likely driven by higher maximum depth in species with the largest depth ranges.) The distribution of depth ranges in meters for each species in the dataset is shown in Fig. 1c, colored by habitat and ordered in ascending order of relative brain size (CNS/ML). In particular, the plot illustrates how species with relatively larger brains tend to live in benthic or variable habitats.

Sociality
The ABH predicts a weak or non-existing relationship between brain size and sociality for cephalopods, as asocial learners do not benefit from a larger group in the way social learners do. This prediction is one of the key differences between the social brain hypothesis and ABH. Consistent with this prediction, whether species were solitary or gregarious was not positively associated with brain size (Fig. 2a). Sociality instead had a somewhat negative effect (-0.21 [-0.58, 0.17]). We also ran an analysis using three categories for sociality rather than the binary measure, with an additional 'in-between' code meant to capture species that appear tolerant of or would associate with other individuals close by (coded as solitary in the binary variable). These include some species that have been observed aggregating in the wild or displaying pair bonding behaviors such as *Abdopus* species[65,66] or that appear unusually tolerant of proximity in lab conditions such as *Rossia macrosoma*[67] and *Sepia bandensis*[68]. The results were broadly similar for social species strictly coded (-0.19 [-0.57, 0.21]). Tolerant species had a slightly higher estimate for brain size (0.18 [-0.24, 0.64]), but interpretation of this result is complicated by the small number of species in this category (11 total) and the heterogeneity of characteristics that could classify species as falling between solitary and gregarious.

Our findings of a somewhat negative effect of sociality on brain size is consistent with the ABH and contrasts with many of the predictions and findings from mammals and other social vertebrates. Sociality in cephalopods is strongly phylogenetically conserved, with schooling present exclusively among decapodiformes (although some squid and cuttlefish species are not social). Solitary and social species can generally be clearly distinguished; however, there are many aspects of sociality such as group sizes and schooling dynamics in the latter that have not been adequately observed or described in the literature. Cannibalism, common among at least some cephalopods, is another factor that may have obstructed the evolution of richer social lifestyles. Taken together, additional field research is needed to draw more fine-grained conclusions about how sociality interacts with cognition and brain size in cephalopods.

Age at sexual maturity
The ABH predicts a weak or non-existing relationship between brain size and age of sexual maturity relative to lifespan. This prediction emerges for the cephalopods because asocial learners need to move from exploration to exploitation faster given that asocial learning is less efficient than social learning. In contrast, for social learning species, the juvenile period is extended and age of sexual maturity is delayed to allow for more time to learn.

In line with this prediction, we found no consistent relationship between brain size and age of sexual maturity (Fig. 2b). On the one hand, maximum recorded age at sexual maturity had a positive effect (0.30 [0.04, 0.53]). On the other hand, sensitivity checks were run with mean and minimum recorded age of sexual maturity; mean was also positive but the estimate more centered around 0 (0.18 [-0.07, 0.39]) and minimum negative with 95% CI including 0 (-0.08 [-0.38, 0.20]). Data on this variable is sparse and somewhat unreliable; as it mostly comes from indirect measures and different methods may be used to determine whether an individual is mature (e.g. body size, egg development in females), there is inconsistency in how age of sexual maturity is identified across species.

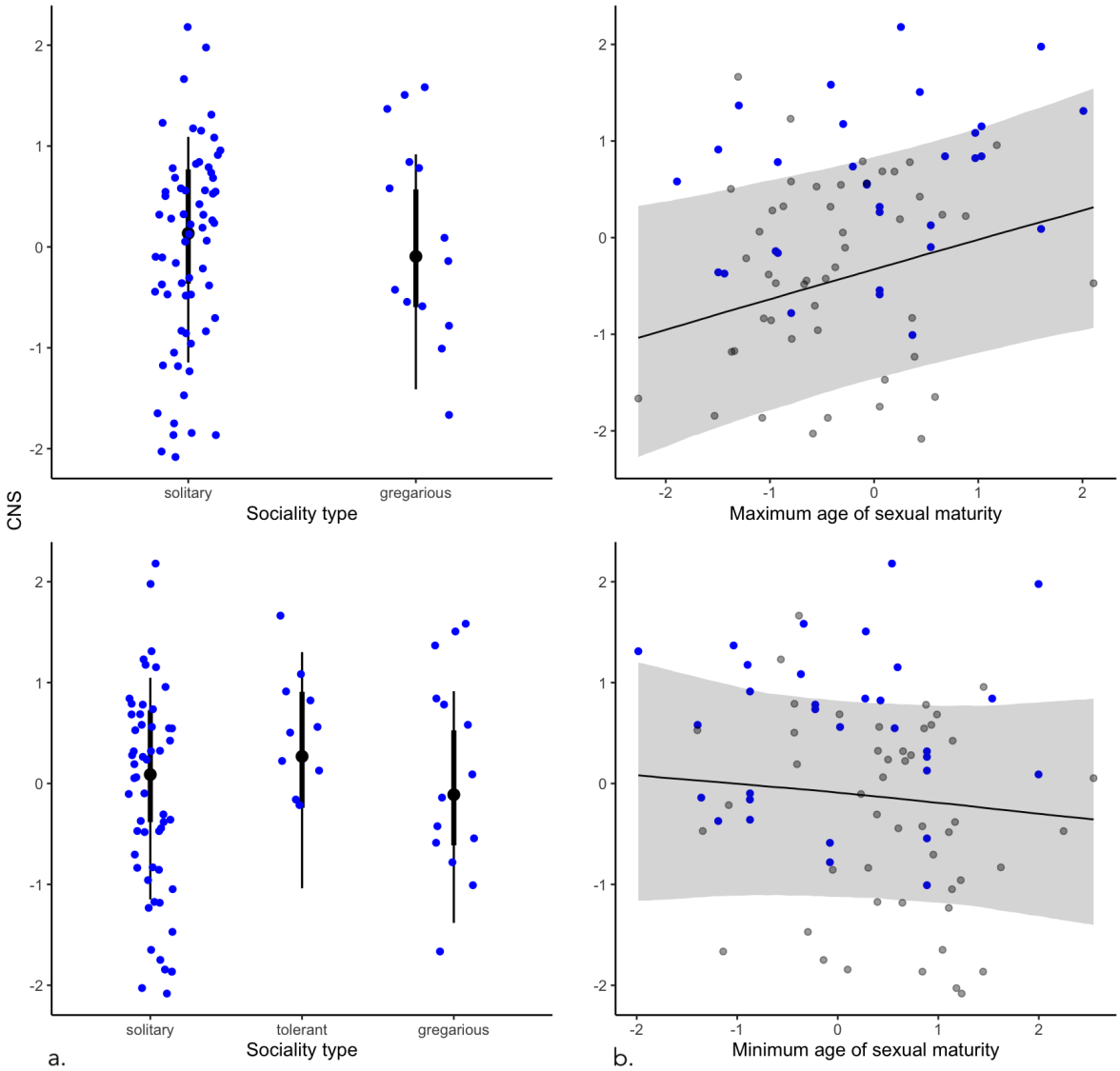

Figure 2. a) Posterior predicted CNS (medians with highest density continuous interval) for each category of sociality. Top shows results for solitary vs. gregarious categories; bottom is solitary, tolerant/in-between, and gregarious categories. CNS is logged and standardized. b) Posterior predicted CNS for maximum age of sexual maturity (top) and minimum age (bottom). Black lines indicate posterior medians and gray shaded area highest density continuous intervals. Blue dots are observed data. Grey dots are imputed values (posterior medians) for species missing data. CNS and ages are logged and standardized.

Behavioral repertoire

The ABH predicts a positive relationship between brain size and behavioral repertoire, as for both social and asocial learners larger brains can store and manage more adaptive information leading to a larger set of flexible behaviors.

Overall, our analyses did not support this prediction as we did not find evidence for a positive relationship between our measures of behavioral complexity and brain size. The effect of the combined cognition measure (summed from cognitive repertoire from lab studies and social behaviors in the wild) was centered around 0 (-0.02 [-0.19, 0.18]). Defense repertoire was also centered around 0 (-0.01 [-0.24, 0.23]). Conversely, the estimate for hunting repertoire was somewhat negative (-0.10 [-0.32, 0.15]). (Fig. 3).

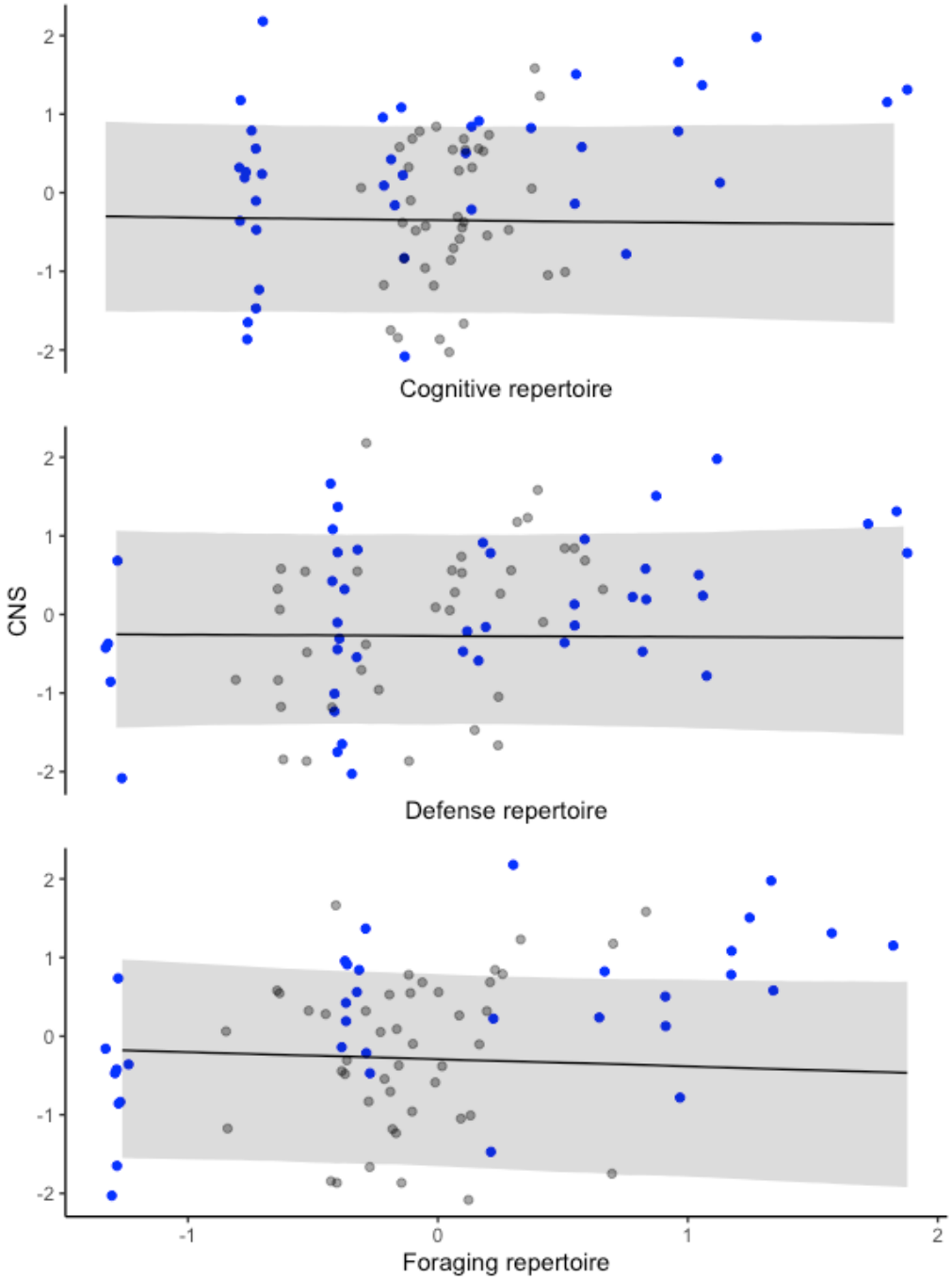

Figure 3. Posterior predicted CNS values for hunting/foraging repertoire. Black lines indicate posterior medians and gray shaded area highest density continuous intervals. Blue dots are observed data. Grey dots are imputed values (posterior medians) for species missing data. CNS and repertoires are logged and standardized.

Therefore, our proxies for behavioral complexity did not show a consistent effect on brain size. This contradicts both our predictions and previous findings of links between behavioral complexity and brain size in other species[7,69]; c.f.[5]. However, as these variables had large amounts of missing data and biases in the distribution of observed behaviors across species, our findings are not conclusive. The need for additional research, in the lab and especially in the wild, is discussed below in the context of overall limitations of the current study.

Summary
Table 2.

	m.meandepth	m.benth	m.dhab	m.phab	m.soc	m.smmean	m.hunt	m.def	m.cog	average
Intercept estimate	-0.335	-0.406	-0.29	-0.218	-0.306	-0.384	-0.316	-0.261	-0.346	-0.318
Intercept 95% CI	-1.449 to 0.806	-1.564 to 0.768	-1.431 to 0.831	-1.345 to 0.933	-1.455 to 0.838	-1.537 to 0.766	-1.653 to 0.789	-1.39 to 1.014	-1.523 to 0.844	
ML estimate	0.658	0.672	0.661	0.667	0.639	0.659	0.682	0.66	0.677	0.664
ML 95% CI	0.499 to 0.812	0.511 to 0.833	0.499 to 0.82	0.51 to 0.819	0.473 to 0.797	0.451 to 0.854	0.514 to 0.838	0.501 to 0.816	0.525 to 0.818	
WoS estimate	0.218	0.134			0.256	0.143				0.188
WoS 95% CI	0.045 to 0.396	-0.031 to 0.304			0.081 to 0.44	-0.082 to 0.351				
Articles read estimate			0.216	0.128			0.239	0.217	0.183	0.197
Articles read 95% CI			0.003 to 0.417	-0.071 to 0.338			0.063 to 0.436	0.035 to 0.404	0.015 to 0.361	
Benthic estimate	0.481	0.577	0.407	0.39	0.48	0.513	0.398	0.382	0.441	0.452
Benthic 95% CI	0.002 to 0.964	0.075 to 1.065	-0.126 to 0.919	-0.102 to 0.896	-0.004 to 0.962	-0.016 to 1.044	-0.091 to 0.889	-0.124 to 0.889	-0.054 to 0.942	
Mean depth estimate	-0.221		-0.266	-0.311	-0.227	-0.282	-0.245	-0.25	-0.233	-0.254
Mean depth 95% CI	-0.382 to -0.062		-0.448 to -0.086	-0.491 to -0.128	-0.39 to -0.067	-0.466 to -0.097	-0.417 to -0.071	-0.42 to -0.083	-0.393 to -0.075	
Combined cognition estimate									-0.02	-0.020
Combined cognition estimate 95% CI									-0.194 to 0.174	
Defense repertoire estimate								-0.009		-0.009
Defense repertoire 95% CI								-0.244 to 0.23		
Diet breadth estimate			-0.093							-0.093
Diet breadth 95% CI			-0.463 to 0.314							
Diet breadth:benthic estimate			0.132							0.132
Diet breadth:benthic 95% CI			-0.273 to 0.516							
Foraging repertoire estimate							-0.096			-0.096
Foraging repertoire 95% CI							-0.323 to 0.146			
Mean lifespan estimate						-0.032				-0.032
Mean lifespan 95% CI						-0.277 to 0.221				
Mean age at maturity estimate						0.183				0.183
Mean age at maturity 95% CI						-0.073 to 0.392				
Predator breadth estimate				0.036						0.036
Predator breadth 95% CI				-0.183 to 0.246						
Predator breadth:benthic estimate				0.241						0.241
Predator breadth:benthic 95% CI				-0.102 to 0.537						
Mean latitude estimate			0.076	0.086		0.046	0.075	0.066	0.039	0.065
Mean latitude 95% CI			-0.081 to 0.23	-0.058 to 0.227		-0.102 to 0.192	-0.064 to 0.213	-0.075 to 0.206	-0.101 to 0.172	
Sociality estimate					-0.215					-0.215
Sociality 95% CI					-0.578 to 0.168					

Coefficient table of mean estimates and 95% CIs for variables (rows) and corresponding models (columns). It should be noted that the 'average' column is mean of posterior means of all models and coefficients should not be interpreted equivalently across models and the meaning will differ depending on included covariates (see code for DAG in Supplementary Information). Remaining coefficients and models are in Supplementary Table 1.

In summary, our findings are inconsistent with social theories of brain evolution[12,17], as solitary vs. gregarious lifestyles did not predict larger brain sizes in our dataset. In contrast with what has been theorized for and received some support among the aforementioned social vertebrates[4,70], age at sexual maturity did not show a consistent positive effect. This suggests that the length of the juvenile period is not a factor in the evolution of cephalopod brains.

Our findings are generally consistent with what can be broadly categorized as 'ecological' theories of brain size evolution (e.g.[6,7]), which are generalized and modeled by the CBH and the ABH. In particular, depth and habitat appeared to be reliable predictors of brain size, with

shallower-living and benthic species tending to have larger brains. If we consider shallower and benthic habitats to be relatively more complex than deep sea and pelagic habitats, this is in line with the idea that environmental variability selects for greater cognitive capacities and larger brains. We also found some support for levels of predation, measured through the breadth of predator taxa, as predicting larger brains, although this variable suffers from missing data and difficulty with accurate measurements for many species. This is consistent with hypotheses of technical intelligence that have emphasized how large brains may coevolve with the ability for innovative and complex behaviors, allowing animals to survive in variable environments and cope with ecological challenges[71,72]. However, a far greater amount of lab and field data would be needed to properly test the predictive value of variables like behavioral innovation rate, which has been shown to predict brain size in birds and primates[6,73]. While our results similarly support some aspects of the cognitive buffer hypothesis[74], i.e. selective pressures for cognitive ability from a variable environment, this predicts that large brains will preferentially be selected in longer-lived species[31], which does not apply well to short-lived coleoid cephalopods. Further research will help clarify the aspects of these different environments that serve as selection pressures, and how these interact with variables such as predation pressure and diet that were less conclusive in our analyses.

Limitations and future directions

A limitation of the current study was the single measurement of brain and body size for the majority of species, so intra-species variability was not taken into account. As we constrained our analyses to species with presently available quantitative brain data, selection bias would be a risk if these particular 'brain data' species are exceptional in relevant characteristics compared to non-sampled species. For instance, shallow-water species might have been easier for researchers to sample in addition to having larger brains and, in turn, possess more complex behavior due to their shallow-water habitats Similarly, smaller species might be less likely to be sampled due to their small sizes and have different behavioral repertoires than bigger species.

The present dataset, which primarily builds on brain data from Wirz[58] and[51,57,58], updated by Chung[75], spans a wide variety of species that are diverse in size and habitat and covers a wide range of families across the major lineages (squid, octopuses, and cuttlefish) within the coleoid cephalopod phylogeny. Therefore, we deem it unlikely that brain size directly influences the probability of sampling, which would be the worst case scenario from a selection bias perspective. Still, research effort did seem to weakly predict larger brains in our statistical models (Table 2). Our dataset includes comparative quantitative brain data for 79 species, which amounts to roughly 10% of the total number (around 820) of extant cephalopod species. Future research using additional reliable and comparable brain data, both for the species in the current dataset and other species without current brain measurement data, should provide additional insight into processes of brain evolution across the cephalopod family tree.

Additionally, although there is extensive behavioral data on a few species, especially the common octopus (*Octopus vulgaris)* and common cuttlefish (*Sepia officinalis*), similar data are lacking for the majority of species. Our measures of ecological and behavioral complexity based on field observations may also not have accurately represented the actual distribution of such behaviors across different species. For instance, among species with available data, our measure of diet breadth (count of taxonomic categories found to be eaten by a particular species) did not correlate strongly with our measure of hunting/foraging behaviors (0.15, p =

0.41). Similarly, defense repertoire was not correlated with breadth of predator taxa (-0.38, $p = 0.15$). Although we controlled for research effort, this might not have been sufficient to account for the extent to which variables like diet breadth, number and variety of predators, foraging strategies, and other behaviors were simply not described in the literature for a large proportion of species in our dataset. There are also biases in the types of observations; as noted above, there are numerous lab studies explicitly on learning capacities and other behaviors in certain species while others had a large amount of literature primarily on fisheries or other topics not related to cognition or behavior. However, this is an issue with any large database project using secondary data not originally collected on topics related to the focus of the database.

Our findings contrast with the link shown by previous research between sociality and brain size among primates and other vertebrate species such as birds. They also did not indicate that a longer juvenile period, which in other species is associated with a period of social learning from parents and conspecifics, predicted a larger brain among cephalopods, which usually die after mating and do not engage in parental care. While our analyses did not support a clear association between larger brains and behavioral complexity, as captured through cognitive measures, conspecific interactions requiring various forms of social cognition, and hunting and defense behaviors, the data for these variables are sparse and require further research in the lab and field. As our analyses used whole brain size as the focal outcome, they also did not take into account measures of brain structure, organization, and neuron numbers which have been shown to relate to variation in behavioral repertoires and complexity in other species[76,77]. Among cephalopods, this includes research on relative lobe size and how these link with ecological factors[51,57,58]. We did find support for effects of ecological variables, particularly habitat and depth, and this likewise should be an avenue for further research that could produce more precise results.

Cephalopods, then, provide a unique comparison to the taxa that have most often been the subject of comparative brain evolution studies[39,53]. In addition to focusing on a previously neglected group in this literature, our study tests – and finds broad support for – predictions explicitly derived from formal modeling of a general theory for the evolution of expanded brains and intelligence[35]. Modeling is an important step in theory development for the study of complex systems[78], and should accompany data collection and collation as we continue to research the evolution of diverse intelligences across the animal kingdom.

Methods

Data collection

Brain and body size data were taken mainly from Wirz[58] and Maddock and Young[57], updated by Nixon & Young[51], combined with a few newer species-specific brain data estimates[75,79–82]. We used brain size measurements from adult specimens of identifiable species (79 total). Data on behavior, ecology, physiology, and other traits were collated from a systematic review of articles written on each species on Web of Science, taking into account alternate species names. The bulk of the data was captured up until November 2020, which was followed up by a more targeted data collection effort for particular species and variables. We also captured and coded data from major books on cephalopod ecology, physiology, and behavior[49,51,83–86];[51].

Due to a lack of data on pre-adult stages, we coded our variables focusing on adult brain and behavior. We did not distinguish between observations of male or female individuals except in cases of sex-specific variables (e.g. male courtship displays).

Variable operationalization
Brain size was operationalized as the total central nervous system (CNS) volume including optic lobes (in millimeters^3) from the sources listed above. Body size was operationalized as the mantle length from the same specimens in millimeters. In the analyses reported here, we use the maximum recorded total CNS volume and, when available, its associated mantle length size. As sensitivity checks, we re-ran main models on available supplementary CNS data (see https://github.com/kcbasava/ceph-brain-evolution/tree/main/sensitivity-checks).

We operationalized the length of the juvenile period/age of sexual maturity through the oldest age at which a species is not observed to be sexually mature measured in number of days, with lifespan (also in days) included in the models for which this was a predictor. We analyze both the maximum and minimum recorded ages. Sociality was measured as a categorical variable with species coded as solitary (avoiding other conspecifics except for mating), gregarious (usual or obligate schooling), or tolerant/aggregative (an in-between category with individuals sometimes observed as congregating outside of reproductive contexts and appearing tolerant of closeby individuals). This was coded as a binary variable in the main analyses with 'tolerant' species coded as solitary/0. Sensitivity checks were run with the three-category measure.

Species were characterized as having benthic or pelagic habitats, with benthic defined as animals living on and/or closely interacting with the seafloor and pelagic animals primarily living in the water column. After further review of these variables, it was decided to create a third category for species observed interacting both with the seafloor and swimming in the water column (demersal/in-between) that would otherwise be classified as benthic. Depth was measured through the minimum and maximum depths in meters at which adult individuals of each species had been recorded, as well as a 4-category variable which classified species as living in shallow waters, undergoing daily vertical migration, migrating to the depth as adults (i.e. ontogenetic migration), and living in the deep sea.

Behavioral complexity was measured through (a) combined social behaviors and cognitive measures, (b) number of defense/antipredator behaviors, and (c) number of foraging behaviors, each used as predictor variables (full description in SI). The combined cognition measure was intended to capture behavioral complexity both as measured through lab studies of abilities such as learning, memory, and problem solving, as well as through field observations of interactions with conspecifics in the wild, e.g. with deception in mating contexts and communication abilities, for species which have not been studied in one or the other context.

Researcher effort was accounted for by including variables for (1) number of articles published on Web of Science for the species name (or alternative names) and (2) articles read during coding of the dataset. The former was used as the standard variable for research effort while the latter was used for variables more likely to be biased due to frequency of observation (i.e. count variables including dietary breadth, number of predators, or foraging strategies).

Statistical models
All analyses are Bayesian multilevel linear regression models and were run using the brms package in R [87], an interface to the probabilistic programming language Stan [88]. They generally follow the operationalization of Bayesian multilevel regression models from

McElreath[89] as implemented in brms by Kurz[90]. All models included brain size (as total CNS volume) modeled as a function of body size (as mantle length). Other variables were included as derived from adjustment sets from a directed acyclic graph (DAG) depending on the focal predictor. The code describing the DAG, including all variables and hypothesized causal paths, are available in the R scripts at https://github.com/kcbasava/ceph-brain-evolution. All variables except for habitat and sociality were standardized (mean centered with a standard deviation of 1) and log-transformed prior to analyses. Priors were chosen to be weakly regularizing. A consensus phylogeny created from the results of the phylogenetic software (discussed in detail in the Supplementary Information) was incorporated as a covariance matrix following the implementation in Kurz[91]. Models were fitted according to the following structure:

```
brm(bf(CNS ~ mi(ML) + mi(X1) + X2 + effort + (1 | gr(species, cov = cormat))) +
        bf(X1 | mi() ~ 1 + mi(ML) + X2 + (1 | gr(species, cov = cormat))) +
         bf(ML | mi() ~ 1 + X2 + (1 | gr(species, cov = cormat))),;
        data = d, data2=list(cormat=cormat),
        prior = c(prior(normal (0,1), class = Intercept),
        prior(normal(0, 0.5), class = b)))
```

where CNS is total brain volume, ML is mantle length , effort is research effort, X_1 is a predictor or predictors with missing data defined by the second bf() formula and X_2 is a predictor or predictors without missing data. 'Cormat' represents the correlation matrix for the consensus phylogeny. Models were run for 8000 iterations. As a robustness check accounting for uncertainty in branch lengths, models were also run over a set of 100 phylogenies sampled from the posterior distribution of the phylogenetic inference analysis (described in detail in Supplementary Information) and the results combined using the combine_models() function in brms.

Sensitivity checks were run using additional measures of brain data and mantle length for species with measures from multiple individuals to ensure broadly similar results were attained.
Sensitivity checks were also run with focal predictors with missing data in the main analyses (age at sexual maturity, predator breadth, diet breadth, hunting repertoire, and defense repertoire) with the missing cases dropped instead of imputed. These analyses did not contradict any of the findings from the imputed analyses (see analyses and supplementary data available at https://github.com/kcbasava/ceph-brain-evolution/tree/main/sensitivity-checks).

Some variables, e.g. communication and reproductive behaviors or hunting behaviors, were aggregated into a single measure to make use of all available observations for each species. A detailed definition for each variable and operationalization in the analyses are provided in the Supplementary Information. While this helped make use of all available data rather than discarding variables, it is likely this aggregation biased these codes towards heavily studied species even after accounting for researcher effort with the number of articles on the species in Web of Science.

Phylogeny
In order to make use of all species for which brain measurements were available, we built a composite phylogenetic topology based on results of prior phylogenetic studies and inferred divergence times with the BEAST2 software[92] using sequence data from GenBank [93]. A

detailed account of the methods for building the phylogeny are in the Supplementary Information. As relationships between coleoid species at more detailed levels than the octopodiforme-decapodiforme split are still uncertain [94,95], we consider our phylogeny to be a rough approximation of a "true" set of evolutionary histories that nonetheless, when properly included in our statistical models, should partly guard against unobserved confounding through shared evolutionary trajectories. An ancestral state reconstruction of relative brain size (logged CNS/ML) using the 'contMap' function from the package phytools in R [96] is shown on the consensus phylogeny in Figure 4. Relative brain size is somewhat phylogenetically conserved, with larger measures appearing among the incirrate octopuses and cuttlefish.

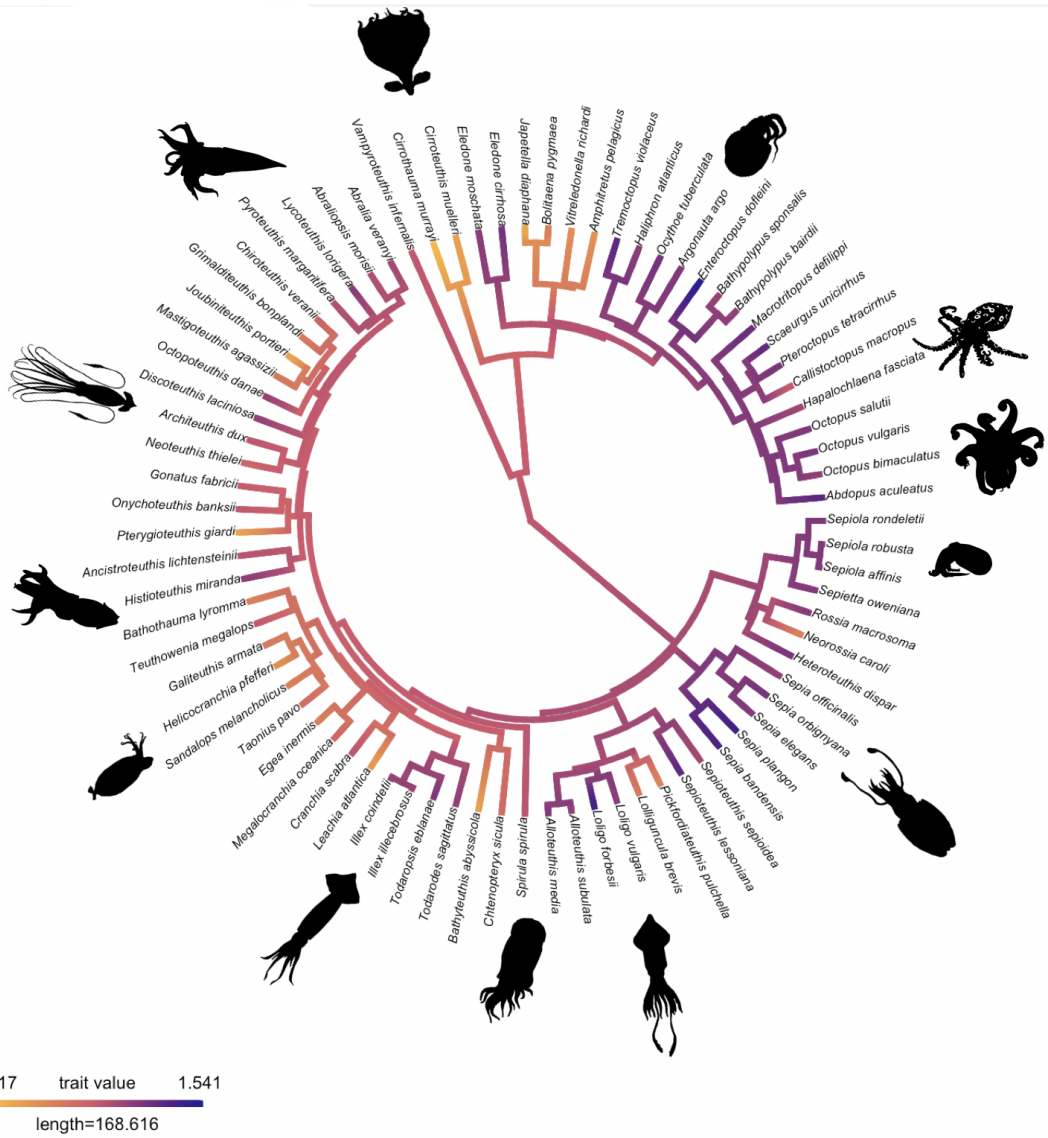

Figure 4. Ancestral state reconstruction of relative brain size (CNS/ML) on a log scale. Images from phylopic.org (Keesey 2024).

Author contributions

KB: Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration
TB: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration

AL: Conceptualization, Methodology, Validation, Investigation, Data curation, Writing – review & editing, Visualization, Project administration
NG: Investigation, Data curation
ZV: Investigation, Data curation
JO: Investigation, Data curation
JM: Conceptualization, Methodology, Validation, Writing – review & editing, Supervision
MM: Conceptualization, Methodology, Validation, Software, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition

Data Availability
Analysis code and data are openly available at www.github.com/kcbasava/ceph-brain-evolution. The pre-registration document can be found at www.osf.io/5dyfz.

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