



# A Total Evidence Phylogenetic Analysis of Pinniped Phylogeny and the Possibility of Parallel Evolution Within a Monophyletic Framework

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In the present study, a series of phylogenetic analyses of morphological, molecular, and combined morphological-molecular datasets were conducted to investigate the relationships of 23 extant and 44 fossil caniforme genera, in order to test the phylogenetic position of putative stem pinniped *Puijila* within a comprehensive evolutionary framework. With *Canis* as an outgroup, a Bayesian Inference analysis employing tip-dating of a combined molecular-morphological (i.e., Total Evidence) dataset recovered a topology in which musteloids are the sister group to a monophyletic pinniped clade, to the exclusion of ursids, and recovered *Puijila* and *Potamotherium* along the stem of Pinnipedia. A similar topology was recovered in a parsimony analysis of the same dataset. These results suggest the pinniped stem may be expanded to include additional fossil arctoid taxa, including *Puijila*, *Potamotherium*, and *Kolponomos*. The tip-dating analysis suggested a divergence time between pinnipeds and musteloids of ~45.16 million years ago (Ma), though a basal split between otarioids and phocids is not estimated to occur until ~26.52 Ma. These results provide further support for prolonged freshwater and nearshore phases in the evolution of pinnipeds, prior to the evolution of the extreme level of aquatic adaptation displayed by extant taxa. Ancestral character state reconstruction was used to investigate character evolution, to determine the frequency of reversals and parallelisms characterizing the three extant clades within Pinnipedia. Although the phylogenetic analyses did not directly provide any evidence of parallel evolution within the pinniped extant families, it is apparent from the inspection of previously-proposed pinniped synapomorphies, within the context of a molecular-based phylogenetic framework, that many traits shared between extant pinnipeds have arisen independently in the three clades. Notably, those traits relating to homodonty and limb-bone specialization for aquatic locomotion appear to have multiple origins within the crown group, as suggested by the retention of the plesiomorphic conditions in early-diverging fossil members of the three extant families. Thus, while the present analysis identifies a new suite of morphological synapomorphies for Pinnipedia, the frequency of reversals and other homoplasies within the clade limit their diagnostic value.

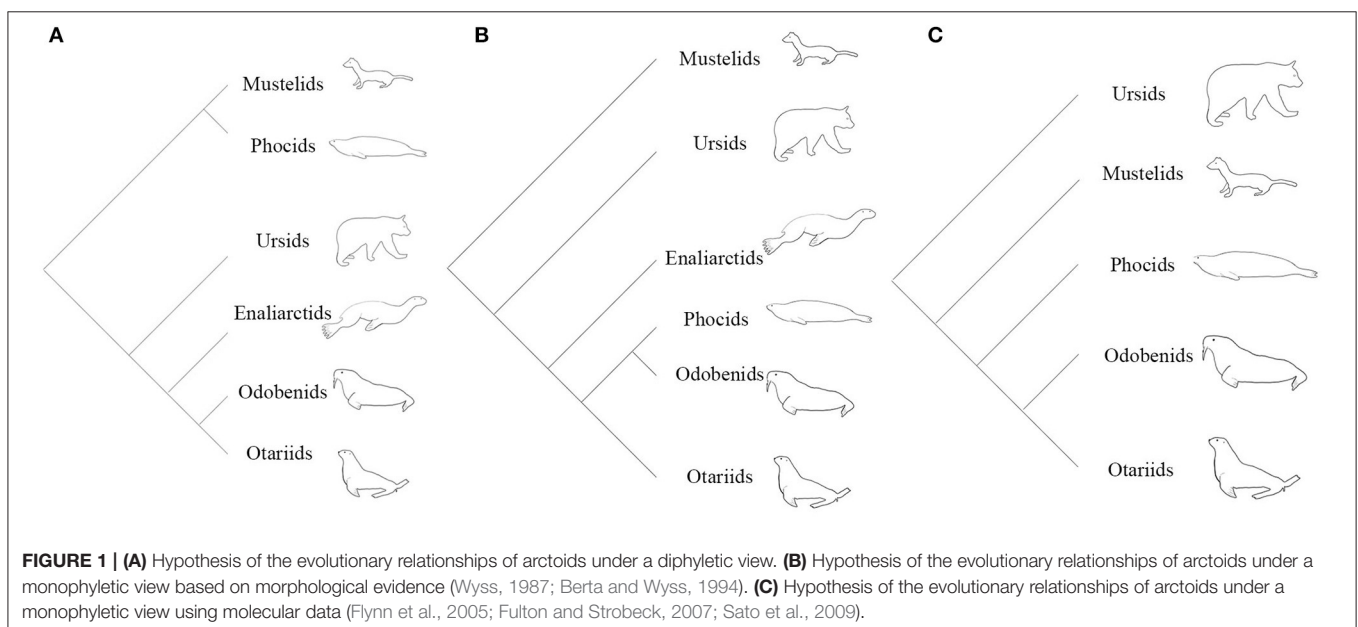
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## INTRODUCTION

From the 1960's until the late 1980's, pinnipeds (seals, sea lions, and walrus) were widely believed to be diphyletic, based partly on the divergent locomotory styles and morphologies observed in extant taxa (Mivart, 1885; McLaren, 1960). A diphyletic view aligns phocids with musteloids (weasels, raccoons, and allies), and grouped otarioids (otariids: fur seals and sea lions; and odobenids: walrus and kin) with ursoids (bears) (**Figure 1A**; Ray, 1976; Tedford, 1976; Repenning and Tedford, 1977; de Muizon, 1982a,b; Wozencraft, 1989; Nojima, 1990). The paradigm shifted when Wyss (1987) provided evidence from inner ear morphology strongly suggesting a monophyletic relationship of phocids, otariids, and odobenids (**Figure 1B**). Wyss' careful observation of this anatomy and subsequent recognition of pinniped homologies corroborated earlier morphological (Weber, 1904; Gregory, 1910; Davies, 1958), cytogenetic (Fay et al., 1967), and biomolecular (Sarich, 1969; Arnason, 1974; Romero-Herrera et al., 1978; de Jong and Goodman, 1982; Miyamoto and Goodman, 1986; Sato et al., 2009) work identifying pinnipeds as monophyletic. From the publication of Wyss (1987) to the present, the vast majority of phylogenetic studies have confirmed Wyss' assertion, regardless if the nature of the evidence was molecular (Dragoo and Honeycutt, 1997; Flynn and Nedbal, 1998; Flynn et al., 2005; Fulton and Strobeck, 2006; Sato et al., 2006; Yonezawa et al., 2009), morphological (Berta and Wyss, 1994; Deméré and Berta, 2002; Kohno, 2006; Furbish, 2015), or a combination of the two (Flynn et al., 2000). However, some morphological (Koretsky et al., 2016), biomechanical (Kuhn and Frey, 2012) and biogeographical (Koretsky and Barnes, 2006) studies continue to uncover evidence questioning the monophyly of pinnipeds, though these studies disregard the wealth of molecular evidence in support of monophyly.

Though pinniped monophyly has been well-supported by both molecular and morphological data, it is not apparent how phocids and otariids developed such disparate morphologies and locomotory modes. A diphyletic origin of pinnipeds serves as a compelling argument to explain the contrasting swimming styles and morphological disparity observed between otariids and phocids (Kuhn and Frey, 2012). Otariids are more ursid-like in general appearance and retain the capability of inverting their hindlimbs on land, allowing them to perform some semblance of quadrupedal ambulatory locomotion (Berta, 2012). When submerged, otariids engage in pectoral oscillations, using their enlarged foreflippers to figuratively fly through the water (English, 1976). The more fusiform phocids are unable to revert their hindlimbs forward on land, and swim using pelvic oscillations, producing thrust underwater via lateral undulations of their pelvic region and alternate protraction and retraction of their hindflippers (Fish et al., 1988; Pierce et al., 2011). The highly autapomorphic *Odobenus rosmarus*, the lone extant member of the once speciose Odobenidae, is not easily accommodated into either group. *Odobenus* is more otariid-like in general appearance, but shares a peculiar suite of features with phocids, not found in otariids (Wyss, 1987; Berta and Wyss, 1994). *Odobenus* displays an intermediary swimming style, using pectoral oscillations at slow speeds and pelvic undulations at high speeds (Gordon, 1981). Interpretation of fossil evidence led diphyletic proponents to identify *Odobenus* as a highly-derived otarioid, a notion supported by molecular studies, though not within the framework of a diphyletic Pinnipedia (Flynn et al., 2000; Fulton and Strobeck, 2007).

The evolutionary relationships advocated by proponents of pinniped diphyletic were initially not subject to the rigor of appropriate cladistic methods (McLaren, 1960). Later studies invoking cladistic methods continued to recover these relationships, though these analyses typically excluded characters



that may have arisen in parallel due to the functional constraints associated with aquatic specialization (Tedford, 1976; de Muizon, 1982a). Pinniped diphyly is supported by a small number of morphological features shared between otarioids and ursids on the one hand, and phocids and mustelids on the other hand (McLaren, 1960; Tedford, 1976; de Muizon, 1982a). The features shared between otarioids and phocids, largely in the postcranial skeleton and auditory region, were disregarded due to their perceived susceptibility to homoplasy (Tedford, 1976), a notion later shown to be untenable within an appropriate phylogenetic framework (Wyss, 1987, 1988). Cladistic analyses of large morphological datasets have unilaterally supported pinniped monophyly (Berta and Wyss, 1994). However, such analyses have had difficulty establishing the relationship of pinnipeds to other arctoids, as their results are typically incongruent with the relationships identified by molecular analyses (e.g., Berta and Wyss, 1994 vs. Bininda-Emonds et al., 1999; Fulton and Strobeck, 2007). This problem is exacerbated by the paucity of fossil remains representing early-diverging pinnipeds that could fill the gap between them and any putative arctoid clade (Deméré et al., 2003).

Since the establishment of pinniped monophyly (Wyss, 1987, 1988; Berta et al., 1989), the most contentious issue in pinniped systematics has been the placement of pinnipeds within Arctoidea. Phylogenetic analyses of morphological data are in disagreement over the sister group of pinnipeds, with musteloids and ursids both presenting compelling cases. Identification of Ursidae as the sister group to pinnipeds was a minor component of early hypotheses of pinniped monophyly (Wyss, 1987; Berta and Wyss, 1994), as the most recent common ancestor of pinnipeds was envisioned as ursid-like. *Enaliarctos*, the earliest-diverging pinnipedimorph known at the time, possesses many features which were thought to characterize ursids ancestrally, including a shelf-like P<sup>4</sup> protocone, a labiolingually-restricted M<sup>1</sup>, and a deep lateral basioccipital embayment for the inferior petrosal sinus (Mitchell and Tedford, 1973; Flynn et al., 1988; Hunt and Barnes, 1994). However, Wolsan (1993) and Kohno (1993, 1994, 1996a) recovered musteloids as the sister group to pinnipeds, a pairing strongly supported by molecular data (Figure 1C; Flynn et al., 2005; Fulton and Strobeck, 2007; Sato et al., 2009, 2012; Doronina et al., 2015).

*Puijila darwini*, uncovered from lacustrine deposits in the High Arctic, was originally proposed to be a transitional pinniped (Rybczynski et al., 2009), filling in the gap between the fully-flipped *Enaliarctos* and terrestrial carnivorans. This hypothesis was based on a relatively small parsimony analysis, employing exclusively morphological characters, investigating the relationships of *Puijila* to terrestrial and semi-aquatic arctoids. However, this interpretation requires a more comprehensive phylogenetic analysis (Diedrich, 2011; Berta, 2012; Boessenecker and Churchill, 2013; Koretsky and Domning, 2014; Koretsky et al., 2016). In the initial analysis (Rybczynski et al., 2009), *Puijila* was recovered in a clade with *Enaliarctos*, *Potamotherium*, and *Amphicticeps*, thereby supporting the notion *Puijila* is either a pinniped, a pinnipedimorph, or an earlier-diverging member of this clade.

However, an extensive sampling of crown-group pinnipeds was not included.

Many comparative analyses of carnivorans, including phylogenetic investigations, have excluded pinnipeds (Bininda-Emonds and Gittleman, 2000), with researchers concerned the extreme aquatic adaptations of pinnipeds may obscure functional patterns across terrestrial carnivorans. Moreover, analyses investigating the interrelationships of pinnipeds and other arctoids have been limited to extant/crown taxa. Morphological analyses have included only broadly-defined “Mustelidae,” “Ursidae,” and/or “Amphicyonidae” as outgroups (Kohno, 1993, 1994; Berta and Wyss, 1994). Assimilating in-group taxa into a hypothetical common ancestor is indeed more prudent than using exemplary taxa (Bininda-Emonds et al., 1998), but still requires many assumptions (e.g., monophyly), which can be easily violated by incompletely preserved extinct taxa.

Excepting Finarelli (2008), which included only a single pinniped species, phylogenetic analyses of fossil arctoids have omitted extant taxa (Wolsan, 1993; Wang et al., 2005). Such analyses have provided valuable insights into the nuanced differences between the stem-ward taxa of each clade. However, without molecular data constraining the topology, it is difficult to retrieve robustly-supported topologies and reconstruct ancestral nodes.

The present work synthesizes these detached lines of inquiry, which are made less incongruous by the inclusion of numerous extinct taxa from the respective arctoid families and subfamilies. A total-evidence tip-dating approach is employed to test the proposed allocation of *Puijila darwini* to the stem of Pinnipedia, and to investigate the evolutionary relationships of and patterns of character evolution associated with early-diverging pinnipeds. The addition of extinct arctoids, and a broad sampling of extant taxa, including both morphological and molecular data, allows for the reconstruction of ancestral nodes to be made from the phylogenetic method itself.

## INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; BSP, Bayerische Staatssammlung für Paleontologie und Historische Geologie, Munich, Germany; CMN, Canadian Museum of Nature, Ottawa, Canada; FMNH, Field Museum of Natural History, Chicago USA; FSL, Département des Sciences de la Terre, Université Claude Bernard, Lyon, France; JODA, John Day Fossil Beds, Kimberly, USA; LACM, Natural History Museum of Los Angeles County, Los Angeles, USA; MGL, Musée Géologique Cantonal, Lausanne, Switzerland; MNHN, Institut de Paleontologie, Museum National d’Histoire Naturelle, Paris, France; NMB, Naturhistorisches Museum Basel, Basel, Switzerland; NMNS, National Museum of Nature and Science, Tsukuba, Japan; NUFV, Nunavut Fossil Vertebrate Collection (housed in CMN); ROM, Royal Ontario Museum, Ottawa, Canada; UOMNH, University of Oregon Museum of Natural History, Eugene, USA; USNM, Smithsonian Institution National Museum of Natural History; UWBM, University of Washington

Burke Museum, Seattle, USA; YPM, Yale Peabody Museum, New Haven, USA.

## MATERIALS AND METHODS

### Selection of Taxa

Appendix 1 in **Supplementary Material** lists the taxa coded for use in the analyses, and identifies which taxa are included in each analysis. Completeness was considered when selecting extinct taxa. For example, *Eotaria*, the earliest-known otariid (Boessenecker and Churchill, 2015; Velez-Juarbe, 2017), was not included, as it is known only from fragmentary mandibular and dental elements (10.29% scored). *Semantor*, a semi-aquatic arctoid with disputed phylogenetic affinities (Orlov, 1933), is similarly known from only post-cranial elements (14.70% scored overall), and was also excluded from the present analyses. A primary goal in the selection of extinct taxa was to sample early-diverging members of each clade (as identified in Wolsan, 1993; Berta and Wyss, 1994; Wang et al., 2005; Finarelli, 2008), following the methodological reasoning of Wang et al. (2005). A representative taxon of every known family within Arctoidea, extinct or extant, is included. See the **Supplementary Information** file for detailed explanations for each included taxon.

Canidae was identified as an ideal outgroup for this analysis, reflecting the sister group relationship between canids and arctoids (Tomiya and Tseng, 2016), and the availability of molecular data for the group. The earliest diverging canids are *Prohesperocyon* and *Hesperocyon*. The latter is well-represented in the fossil record, and does not display the specializations observed in later-diverging canids, so it is included in the present study. *Canis lupus* is included as the lone extant canid.

### Total Evidence Dating

To date the phylogeny and coestimate the times and evolutionary rates, a “total-evidence dating” approach, was employed (Pyron, 2011; Ronquist et al., 2012b, 2016; Gavryushkina et al., 2016; Lee, 2016; Zhang et al., 2016; Wang et al., 2017). Also known as fossil-tip calibration, this approach allows for the simultaneous analysis of extant and extinct taxa, integrating known age ranges of extinct taxa (directly associated with fossil tips) to infer phylogeny, divergence times, and macroevolutionary parameters (Ronquist et al., 2012a). Furthermore, employing a fossilized birth-death model into a tip-dating analysis allows for the incorporation of information concerning speciation, extinction, and sampling processes (Zhang et al., 2016).

### Molecular Data

Following Sato et al. (2009), nucleotide sequences of five nuclear coding genes were obtained—APOB (Apolipoprotein B), BRCA1 (Breast cancer 1, early onset), RAG1 (Recombination activating gene 1), IRBP (Interstitial retinol binding protein 3), VWF (Von Willebrand factor)—for a selection of extant arctoids (see Appendix 2 in **Supplementary Material**). The sequence data were downloaded from GenBank (NCBI, and accession numbers are listed in **Table S3**). Sequences were aligned using the MUSCLE alignment tool in Mesquite (Maddison and Maddison,

2015). To create identical lengths of each individual sequence for each taxon, sequences were manually trimmed in regions that were poorly aligned and/or displayed >50% gaps for a specific column. This ensures that when all five genes are analyzed together, homologous sites for each gene are aligned. Each aligned gene was then allocated to a discrete partition within the dataset. Data was partitioned into six units—Morphological, APOB, BRCA1, RAG1, IRBP, VWF. The Mk model was applied to the Morphological partition. To determine the evolutionary models of best fit for each data partition of molecular data, marginal likelihoods for each available model were calculated and compared separately for each partition using the stepping stone method (Xie et al., 2010), a path sampling method which obviates the controversial use of the harmonic mean method to estimate likelihood (Fan et al., 2010). **Table S2** lists the models and variants that were considered, and their marginal likelihood scores when subject to a Markov Chain Monte Carlo analysis of 5,500,000 generations and 50 steps. The models with the highest average marginal likelihood score (averaged between the two runs), were selected. The GTR + gamma model was selected for VWF, APOB, and BRCA1, and the GTR + invgamma model was selected for RAG1 and IRBP. The models-of-best-fit were later applied to their relevant data partitions in the Bayesian analyses.

Molecular data was included for at least one taxon from each extant caniform family—Canidae (*Canis lupus*), Ursidae (*Ursus arctos*), Mephitidae (*Mephitis mephitis*), Ailuridae (*Ailurus fulgens*), Procyonidae (*Procyon lotor*), Mustelidae (*Gulo gulo*, *Lontra canadiensis*, *Enhydra lutris*, *Neovison vison*, *Taxidea taxus*), Odobenidae (*Odobenus rosmarus*), Phocidae (*Cystophora cristata*, *Erignathus barbatus*, *Halichoerus grypus*, *Mirounga angustirostris*, *Monachus monachus*, *Phoca vitulina*), and Otariidae (*Arctocephalus* sp., *Callorhinus ursinus*, *Eumetopias jubatus*, *Otaria byronia*, *Zalophus californianus*). The inclusion of taxa was based on the availability of their selected genes in GenBank. Gaps and missing characters were treated as missing data. *Canis lupus* was specified as the outgroup.

### Morphological Data

Eighty-two craniomandibular characters, fifty dental characters, and seventy-two postcranial characters were coded when possible for all taxa in the analysis. While some characters are novel, the majority of characters were derived from previous phylogenetic analyses of Carnivora, including those focusing on pinnipeds (Berta and Wyss, 1994; Kohno, 1996a,b, 2006; Deméré and Berta, 2001, 2002, 2005; Boessenecker and Churchill, 2013, 2015, 2018; Amson and de Muizon, 2014; Churchill et al., 2014; Furbish, 2015), musteloids (Bryant et al., 1993; Wolsan, 1993; Ahrens, 2014; Valenciano et al., 2016), arctoids (Tedford et al., 1994; Wang et al., 2005; Finarelli, 2008), and carnivorans more broadly (Wyss and Flynn, 1993; Wesley-Hunt and Flynn, 2005; Spaulding and Flynn, 2012; Tomiya and Tseng, 2016) (see Appendix 1 in **Supplementary Material** for full character list). Many of these characters were then modified, either by editing existing character states or by adding character states, to better reflect the diversity of these characters across arctoids. All changes are noted in the **Supplementary Information File**.



All taxa were specifically coded for this study (Appendix 2 in **Supplementary Material**).

Some phylogenetic analyses of pinnipeds (Deméré and Berta, 2002) have attempted to quantify and discretize characters that gauge nuanced differences in size and/or shape of morphological features, an approach followed in the present analysis. Further work on the morphological characters used in the study of extinct carnivorans should use statistical techniques to test the discretization or “binning” of different character states (Prieto-Marquez, 2010; Zou and Zhang, 2016).

A representative from every known arctoid family was coded, including members of the extinct Amphicyonidae, Oligobuninae and Desmatophocidae (**Supplementary Table 1** in **Supplementary Material**). When possible, adult male specimens were selected for character coding, due to the high sexual dimorphism displayed in many modern (Gittleman and Valkenburgh, 1997) and extinct arctoids (Hunt and Skolnick, 1996; Cullen et al., 2014).

To code their character states, specimens representing the extinct taxa were observed personally. Data for certain characters were also gathered from the literature if not discernible in the specimens available to us. Those concerning the internal cranial anatomy were inferred from video files of CT scans spanning the different axes of the cranium (from [www.digimorph.org](http://www.digimorph.org)) and the literature (Ahrens, 2014; Geraads and Spassov, 2016; Grohé et al., 2016).

## Analysis

The total-evidence tip-dating analysis was initially run in MrBayes v3.2.6 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) for 10,000,000 generations, with a sampling frequency of 1,000 and a diagnostic frequency of 1,000. To ensure convergence upon similar results, two independent runs of MCMC (Markov-chain Monte Carlo) were specified for each analysis, with four chains (three hot and one cold) per run. Stationarity and convergence of the posterior probabilities were gauged using Tracer v1.6 (Rambaut, 2007) for OSX. Convergence of parameters was identified when the plot of the log likelihoods (“the Trace line”) varied about a constant value. After accepting convergence, runs were considered sufficiently long when the effective sample sizes (ESS's) for each trace rose above 200. AWTY (Wilgenbusch, 2004) was offline as of this analysis, so no test of convergence of tree topologies was used, though analyses were only terminated when the average standard deviation of split frequencies was  $<0.01$ . Inspection of the trace plots also allowed us to identify the burn-in of each analysis, which was subsequently discarded. Following termination of the runs and discarding of the burn-in, the consensus tree showing all compatible clades was requested (contype = allcompat).

A relaxed clock model was implemented to account for evolutionary rate variation across branches and over time. The clock rate was associated with a lognormal prior with a mean of  $-7.0$  and a standard deviation of  $0.6$  on the natural logarithm scale. The analysis specified an independent gamma rates model, and the variance increase parameter had an exponential prior with rate 10. The fossilized birth-death model was employed (Heath et al., 2014), with the following priors: speciationpr = exp(10), extinctionpr = beta(1,1), fossilizationpr = beta(1,1).

The extant sample proportion was estimated to be 0.085. Treeagepr was set at 45, following Matzke and Wright (2016). The full script for this analysis is available in Appendix 3 in **Supplementary Material**.

Fossil stratigraphic ages, used to introduce time intervals for fossil samples, are listed in Appendix 4 in **Supplementary Material**. Fossil ages include ranges of uncertainty.

Ancestral character state reconstruction (ACSR) was performed for selected characters (those identified as possible pinniped or pinnipedimorph synapomorphies and homoplastic characters in this and other analyses) under the maximum likelihood approach using Mesquite v. 3.04. The Trace Character History function was applied to the phylogenetic tree recovered from total-evidence tip-dating, with the morphological characters used as the source of stored characters. The mK1 model was selected as the model of character state evolution, with equal probability for any character change. ACSR was used to identify the likely plesiomorphic condition for each character at the base of Pinnipedia, and to identify any possible reversals or instances of parallel trait development within the clade.

## Parsimony Analysis of Combined Morphological-Molecular Dataset

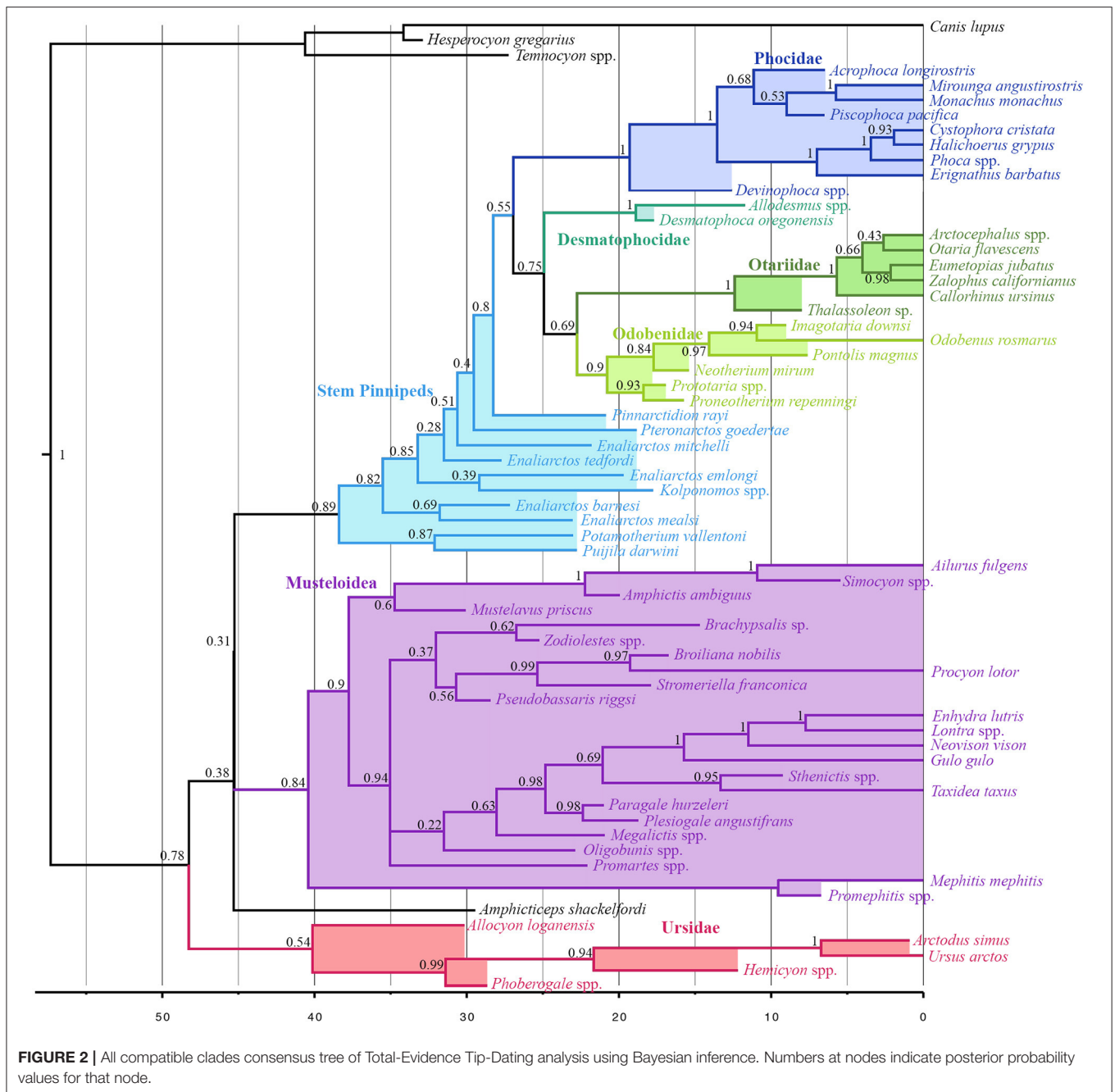
Parsimony analysis was performed on the same dataset with the same outgroup using TNT 1.1 (Goloboff et al., 2008). One thousand replicates of random addition sequences were requested, followed by 500 iterations of tree bisection reconnection (TBR) and parsimony ratchet. Bootstrap support values (BS) were also obtained using TNT, using symmetric-resampling frequencies and 1,000 replicates.

## RESULTS AND DISCUSSION

### Total-Evidence Dating

Musteloids are identified as the sister group to pinnipeds ( $pp = 0.31$ ), and *Puijila* and *Potamotherium* are identified as the sister clade to Pinnipedimorpha ( $pp = 0.89$ ). Otariids and Odobenids are recovered as sister taxa ( $pp = 0.69$ ), and desmatophocids are identified as the sister group to the otariid-odobenid coupling ( $pp = 0.75$ ), to the exclusion of phocids. The present analysis indicates a divergence date between pinnipeds and musteloids in the Eocene, ranging from the Ypresian to the early Bartonian (95% highest posterior density interval 41.17–50.3 Ma) (**Figure 2**). Divergence time estimates for selected nodes are listed in **Table S3**.

Divergence time estimates within crown group Pinnipedia produced by the present analysis do not stray wildly from those posited by other analyses, and in fact recover a divergence between Phocidae and Otarioidea ( $\sim 26.94$  Ma) roughly midway between those of Arnason et al. (2006) on the one hand, and Higdon et al. (2007) and Fulton and Strobeck (2010) on the other. The present analysis identifies an early Miocene ( $\sim 22.76$ ) split between Otariidae and Odobenidae, in agreement with that of several other analyses (Higdon et al., 2007; Yonezawa et al., 2009; Nyakatura and Bininda-Emonds, 2012), while other analyses using node calibration have recovered a later divergence date inconsistent with the ages of the earliest



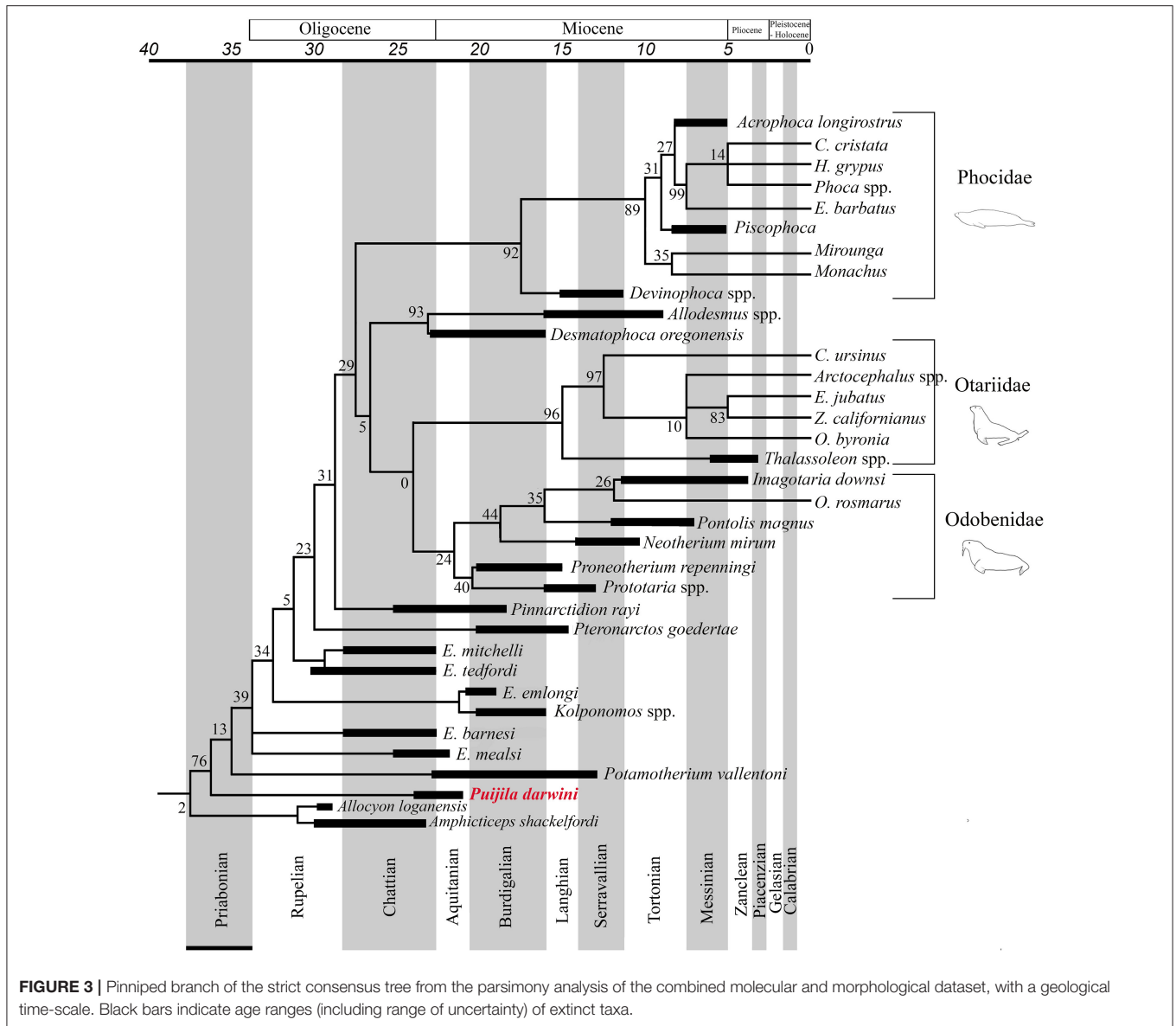
odobenid, *Proneotherium* (Fulton and Strobeck, 2010). Beyond the crown pinniped radiation, the present investigation identifies older divergence times than many other analyses employing node- or tip-dating (excepting Arnason et al., 2006).

On the other side of the pinniped-musteloid split, the oldest incontestable pinniped fossils appear in the earliest Chattian (Berta, 1991; Prothero et al., 2001), far later than both the estimated early-to-mid Eocene split from musteloids, and the estimated ~38.41 Ma divergence time between *Puijila*/*Potamotherium* and all later-diverging pinnipedimorphs (Berta, 1991; Berta and Wyss, 1994). This long gap would

allow plenty of time for the establishment of morphological characteristics reflecting the pronounced level of aquatic adaptation exhibited by *Enaliarctos* (Berta and Ray, 1990), ostensibly following a long initial phase of evolution in a non-marine setting represented by *Puijila* and *Potamotherium*, from lacustrine and fluvial deposits, respectively.

### Pinnipedimorph Taxonomy

The Pinnipedimorpha was erected by Berta (1991) and includes *Enaliarctos* and all of its descendants, including a monophyletic crown-group Pinnipedia, which is strongly



supported in all phylogenetic analyses performed in the present study. This study finds *Puijila* and *Potamotherium* to be members of this lineage that diverged prior to *Enaliarctos*, suggesting that a more inclusive taxonomic definition is warranted. All phylogenetic analyses in the current study recover a monophyletic group that includes crown group pinnipeds and the stem pinnipeds recognized here (*Puijila*, *Potamotherium*, *Kolponomos*, *Enaliarctos*, *Pteronarctos*, *Pinnarctidion*). A monophyletic Pinnipedia is restricted to crown group pinnipeds in both analyses. The reasonably strong support for a monophyletic *Puijila* + *Potamotherium* + Pinnipedimorpha in both phylogenetic analyses suggests *Puijila* and *Potamotherium* may confidently be identified as stem pinnipeds. *Amphicticeps shackelfordi* and *Allocyon loganensis*, a pair of taxa previously identified as possible early-diverging members of the pinniped divergence (Tedford et al., 1994;

Rybczynski et al., 2009), are also recovered along the pinniped stem in the parsimony analysis (**Figure 3**), though this placement is very poorly supported (BS = 2).

*Puijila* and *Potamotherium* do not possess many of the conventional pinniped synapomorphies, but as potential stem pinnipedimorphs, they should not be expected to possess these features. The present Bayesian analysis suggest the features of modern pinnipeds arose sequentially, as observed in many other secondarily aquatic tetrapods (Hall, 1999), rather than as an integrated package.

Ten synapomorphies were identified for a clade of *Potamotherium* + *Puijila* + pinnipedimorphs (**Table 1**), eight of which are identified (> 50% likelihood) at the base of the clade in the ACSR analysis. Unsurprisingly, it is the basicranial region that supports the phylogenetic affinities of *Puijila* and *Potamotherium*, as half of these possible synapomorphies relate to

**TABLE 1** | Synapomorphies of the clade *Puijila* + *Potamotherium* + Pinnipedimorpha, as identified in the parsimony analysis of morphological data.

**Synapomorphies of *Puijila* + *Potamotherium* + Pinnipedimorpha (This study)**

- 1. Postorbital constriction**
2. Lacrimal, size
- 3. Postglenoid foramen**
- 4. Pseudosylvian sulcus**
- 5. Round window size**
- 6. P<sup>4</sup>/M<sup>1</sup> relative size**
7. M<sup>1</sup>, postprotocrista
- 8. M<sup>2</sup>, metaconule**
- 9. P<sub>4</sub> accessory cusps**
- 10. M<sub>1</sub>, metaconid mesiodistal position**

*Bolded characters are those that record >50% likelihood for the internode toward the base of Pinnipedia in the ACSR analysis employing maximum likelihood, as applied to the topology recovered from the Bayesian total-evidence tip-dating analysis.*

the basicranial region. Unfortunately, data from the basicranial region is incompletely known from many fossil specimens, as the majority of basicranial characters are not preserved or are difficult to access. As these regions are of significant phylogenetic utility, conclusions on the precise phylogenetic relationships of early-diverging fossil pinnipeds may be reinterpreted once such data becomes available. Preservational biases have occasionally drastically misled identifications of fossil specimens (Donoghue and Purnell, 2009; Pattinson et al., 2014), and they can cause directional shifts in phylogenetic analyses (Sansom and Wills, 2013). Fossil specimens may appear to lack later derivations or specializations associated with more crown-ward clades, and thus, may erroneously be shifted toward the stem (Sansom, 2014).

Many previous phylogenetic analyses identifying *Potamotherium* as a mustelid have been limited in their observations to just a handful of specimens (Wyss, 1987; Bininda-Emonds and Russell, 1996; Wang et al., 2005; Finarelli, 2008) or relied on Savage (1957) thorough description of the taxon (Furbish, 2015). The pinnipedimorph affinities of *Potamotherium* become increasingly apparent upon inspection of additional undescribed material of *Potamotherium* from the collections at NMB, MNHN, and FSL. *Potamotherium* displays several polymorphic characters, with the derived states commonly representing pinnipedimorph synapomorphies. The variable appearance of these pinnipedimorph synapomorphies suggests a transitional morphology between terrestrial arctoids and pinnipedimorphs. These features include: presence of large antorbital process, mandible deepest anteriorly, reduction of the fossa for the tensor tympani, and presence of a palatal midline ridge.

Although the group Pinnipedimorpha is well-supported, the details of the evolution of the stem lineages are less well-resolved. For example, there is considerable cranial and dental diversity between different species of *Enaliarctos* (Cullen et al., 2014; the present study), and significant taxonomic revision of the genus, with comparison to other stem pinnipeds overlapping *Enaliarctos*

in age, may be warranted. Despite superficially appearing less aquatically-specialized than *Potamotherium*, *Puijila* shares many traits with *Enaliarctos* to the exclusion of *Potamotherium*, though the similarities are not sufficient to recover a closer relationship between the two in our phylogenetic analyses. Many of these traits are also observed in otarioids in general, but not phocids, including: a thin, projecting tympanic crest, an inflated and somewhat rounded caudal entotympanic, and presence of an alisphenoid canal. Specifically, the tympanic crest and tympanic bulla of *Puijila* strongly resemble those of *Enaliarctos emlongi* and *Enaliarctos mealsi*. We also identified the shared presence of an intrabullar septum in *Puijila*, *Enaliarctos emlongi*, and *Enaliarctos mealsi*. Additional traits found in *Puijila*, *Enaliarctos*, and later-diverging pinnipedimorphs, to the exclusion of *Potamotherium*, include: absence of I<sub>1</sub>, a reduced M<sub>1</sub> metaconid, presence of sharp ventral keel on the axis, and presence of a cylindrical lesser tuberosity of the humerus.

The presence/absence of the alisphenoid canal has been considered as a character of significant phylogenetic utility (Tedford, 1976; Koretsky et al., 2016). The alisphenoid canal carries multiple structures, including a branch of the external carotid artery, likely protecting it from occlusion during contraction of the pterygoideus muscle (Ewer, 1973). Accordingly, the alisphenoid canal may have been lost in taxa whose carotid canals lie closer to the orbit, so that the external carotid artery is largely unexposed to the adjacent musculature. This is borne out by mustelids and mephitids, who display a reduced post-canine dentition, and in phocids, who possess large orbits. While it appears unlikely an organism could have lost the alisphenoid canal and subsequently regained it, we cannot, a priori, rule such a scenario out. Thus, the character was not specified as irreversible in our analysis, though we do admit a reversal to the presence of the canal seems unlikely. Within the topology produced by the TEA, we can assume the loss of the alisphenoid canal represents an autapomorphy for *Potamotherium*, rather than a synapomorphy of a hypothetical *Potamotherium* + Phocidae clade (de Muizon, 1982a; Koretsky and Rahmat, 2015). It is likely the alisphenoid canal was lost multiple times in arctoids, including at least once in phocids, mephitids, the clade containing mustelids + procyonids, and *Ailuropoda*, respectively.

## Reappraisal of Pinniped Synapomorphies

Pinnipedia (Illiger, 1811) encompasses the last common ancestor of otarioids and phocids, and all of its descendants (Berta and Wyss, 1994). Wyss (1987) and Berta and Wyss (1994), suggested reversals were likely more common than convergence throughout the early evolutionary history of pinnipeds. This view was based on tree topologies in which Phocidae was recovered as the sister group to Odobenidae, and Ursidae was identified as the sister group to pinnipeds. Such a view has become less tenable as molecular analyses have revised our interpretation of these relationships. Many of these putative reversals may now be reinterpreted, in light of the present analysis. Reversals now appear less common than convergences within pinnipeds, as the ACSR analysis identifies over twice as many likely parallelisms



( $n = 30$ ; interpreted as a trait that arises at least once in multiple crown group clades) as likely reversals ( $n = 14$ ), and a few of these reversals are in fact identified as arising in parallel in multiple crown group clades (Table S4). This notion is also supported by the morphology of the early-diverging fossil representatives of the three extant pinniped families—*Prototaria* (or *Proneotherium*), *Eotaria*, and *Devinophoca*. In spite of their possession of odobenid, otariid, and phocid synapomorphies, respectively, these taxa also possess a suite of primitive characters, lacking some of the aquatic specializations previously used to define Pinnipedia.

In light of the recent discovery of fossils attributable to *Prototaria*, *Proneotherium*, *Eotaria*, and *Devinophoca*, it appears that previously cited pinniped synapomorphies are more variable in distribution among crown group pinnipeds than previously believed, and may not define the base of Pinnipedia. Table 2 lists all previously proposed synapomorphies of crown pinnipeds (Pinnipedia), and notes if the early-diverging fossil crown members of each pinniped family display the ancestral or derived character state, and the likelihood the synapomorphy is present at the identified at the base of pinnipedia based on the ACSR of the tree derived from the total-evidence tip-dating analysis. The ancestral state is observed at least once in a crown member for 11 of the 16 characters, and seven of 16 of these features are identified as unlikely to characterize the base of Pinnipedia using ACSR. The five characters that do not display retention of an ancestral state are postcranial characters that are poorly sampled for these extinct taxa, many of which are only known from skulls, mandibles, and/or a few postcranial elements. The appearance of an ancestral state in any of these fossil forms could theoretically represent an anomalous derivation or reversal. However, if early-diverging

representatives from more than one family retain the ancestral condition, then it is equally parsimonious to assume the derived condition did not characterize the base of Pinnipedia. As Table 2 demonstrates, this latter scenario describes six of the 16 characters. It must be assumed these numbers would increase if there were less missing data (currently only 44/80 total possible codings).

The following features have been used to delineate a monophyletic Pinnipedia to the exclusion of the stem “pinnipedimorphs” *Enaliarctos*, *Pteronarctos*, and *Pacificotaria*: pit for tensor tympani absent, I<sup>3</sup> lingual cingulum absent, M<sub>1–2</sub> trigonid suppressed, nasolabialis fossa absent, antorbital process large, P<sup>4</sup> protocone shelf absent, P<sup>4</sup> one- or two-rooted, and M<sub>2</sub> absent (Berta and Wyss, 1994).

The absence of the pit for the tensor tympani does appear to be a synapomorphy of crown pinnipeds (Wyss, 1987; Berta and Wyss, 1994), as the tensor tympani appears to insert on the Eustachian canal in all extant pinnipeds sampled. However, Wesley-Hunt and Flynn (2005) identified a transitional state in *Pteronarctos*, in which the fossa for the tensor tympani is present, but only shallowly excavated into the promontory. Likewise, the fossa for the tensor tympani is greatly reduced in *Puijila*, several specimens of *Potamotherium* (Mitchell and Tedford, 1973; Pers. Obs.), and multiple species of *Enaliarctos* (Berta, 1991). CT data of the inner ear of early-diverging otariids, phocids, and odobenids should clarify the timing of this transition to determine if the fossa for the tensor tympani was lost multiple times.

Lingual cingulum of the I<sup>3</sup> is retained in *Prototaria* (Kohn, 1994; Kohn et al., 1995) and *Thalassoleon* (Deméré and Berta, 2005). An unreduced M<sub>1</sub> metaconid or trigonid is retained in *Eotaria* (Boessenecker and Churchill, 2013). The nasolabialis

**TABLE 2 |** List of previously proposed synapomorphies of crown group Pinnipedia (Berta and Wyss, 1994), and their occurrence in select fossil pinnipedimorphs.

Previously proposed pinniped synapomorphies	<i>Enaliarctos</i>	<i>Prototaria</i>	<i>Proneotherium</i>	<i>Thalassoleon</i>	<i>Eotaria</i>	<i>Devinophoca</i>	% likelihood trait appears at base of Pinnipedia (ACSR)
Loss of pit for tensor tympani	0	?	0	?	?	?	96.68%
I <sup>3</sup> Lingual Cingulum	0	0	1	0	?	?	76.71%
Reduced m1 metaconid	0	?	1	?	0	?	20.63%
(12)Nasolabialis Fossa Absence	0	0	0	0	?	1	4.01%
(13)Fossa muscularis absence	0	0	1	1	?	1	72.29%
Antorbital Process Large	0	1	1	1	?	0	<0.1%
P <sup>4</sup> Protocone Shelf	0	0	0	1	?	0	9.11%
P <sup>4</sup> 1- or 2-rooted	0	0	0	1	?	0	1.14%
m2 absence	0	0	0	1	0	1	1.08%
Five Lumbar Vertebrae	0	?	?	?	?	?	51.71%
Olecranon flattened and expanded	0	?	?	1	?	1	86.26%
Radius, expanded distal half	0	?	?	1	?	?	99.39%
Pubic symphysis unfused	0	?	?	1	?	?	87.91%
Fovea for teres femoris	0	?	0	1	?	1	26.40%
Greater femoral trochanter larger and flattened	0	?	1	1	?	1	97.60%
Tibia-Fibula Fusion	0	?	0	0	?	?	99.96%

fossa appears to have been lost multiple times in pinnipeds, as it is present in a stem otariid (*Thalassoleon*), multiple fossil odobenids (*Proneotherium* and *Imagotaria*), and a possible desmatophocid (*Pinnarctidion*). Polarity for a large antorbital process must now be reversed, and the character can be conceived of as a possible synapomorphy for otarioids, with further derivation in both otariids and odobenids. A protocone shelf of the  $P^4$  is retained in *Devinophoca* and *Proneotherium* (Churchill and Clementz, 2016). Reduction of the number of roots of  $P^4$  (<3) appears to be a synapomorphy of pinnipeds, however, *Devinophoca* may display a transitional stage in which the posterior root is bilobed, though the roots are nevertheless well-merged (Koretsky and Holec, 2002). A similar  $P^4$  root morphology is observed in *Proneotherium* and *Neotherium*. The  $M_2$  is retained in *Pontolis* (Deméré, 1994), *Eotaria* (Boessenecker and Churchill, 2013), and even atavistically reappears in extant otariids (Drehmer et al., 2004).

Of these proposed synapomorphies, only absence of the fossa for the tensor tympani and reduction of  $P^4$  roots appear to definitively define the node at the base of Pinnipedia. Berta and Wyss (1994) also listed a set of ambiguous postcranial synapomorphies of Pinnipedia, though their presence or absence in *Pteronarctos* and several species of *Enaliarctos* cannot be asserted without postcranial remains. These are: five lumbar vertebrae present, flattened and posteriorly expanded olecranon process, expanded distal end of radius, pubic symphysis unfused, loss of fovea teres femoris, greater trochanter of femur lost. These synapomorphies have not been discovered in pinnipedimorphs, nor have the plesiomorphic conditions been identified in any fossil pinnipeds. However, some of these are approached by *Potamotherium* and *Enaliarctos*, who display somewhat expanded distal radii, somewhat expanded greater trochanters, and a reduced fovea teres femoris. Unsurprisingly, many of these features are thought to be related to aquatic adaptation—general flattening of the long-bones, posterior expansion of the olecranon process, loss of the fovea teres femoris—as they are observed homoplastically in other clades of aquatic mammals (Gingerich et al., 1990, 1994).

Another more inclusive clade than the Pinnipedimorpha is also recognized—Pinnipediformes (Berta, 1994). This group encompasses *Pteronarctos* and Pinnipedia, to the exclusion of *Enaliarctos* (Berta, 1994). Four additional unambiguous synapomorphies were identified for Pinnipediformes: absence of lacrimal-jugal contact, maxilla contributes heavily to orbit, embrasure pit of  $P^4$ - $M^1$  shallow or absent, mastoid process in close proximity to paroccipital process and connected by a ridge.

The extent of the lacrimal is difficult to ascertain in fossil pinnipeds and their ancestors, as the lacrimal becomes well-fused to surrounding bones in ontogeny. It appears likely this is a pinniped synapomorphy. The discovery of juvenile specimens displaying the presence or absence of a lacrimal in *Puijila* or *Enaliarctos* could confirm or undermine this contention. The maxillary contribution to the orbit is also likely a pinniped or pinnipediforme synapomorphy, but fusion of these elements in *Enaliarctos* and *Puijila* precludes certain determination. While the embrasure pit of *Proneotherium* is

reduced (Boessenecker and Churchill, 2013), it is nevertheless present, while all extant pinnipeds observed lack an embrasure pit outright. In phocids, the mastoid and paroccipital processes are widely separated, and the polarity of this character should be reversed, so it is considered a synapomorphy of otarioids.

Another proposed synapomorphy of Pinnipedia is the presence of prominent orbital vacuities (Wyss, 1987; Berta, 1991), which are unossified spaces on the medial orbital wall (Wyss, 1987). The presence of orbital vacuities appears to be unique to crown pinnipeds. The orbital vacuities are similar in phocids and otariids, but are placed far posteriorly in *Odobenus* (Kohno, 2006), though fossil walrus do possess a pinniped-like orbital vacuity (Deméré and Berta, 2001). Though similarly placed, the otariid orbital vacuity is of a different configuration than the phocid orbital vacuity (Wozencraft, 1989; Bininda-Emonds and Russell, 1996), and for that reason, Berta and Wyss (1994) speculate on an independent origin of orbital vacuities in the three pinniped families, a hypothesis supported by the present phylogenetic analysis. Orbital vacuities are absent in *Pinnarctidion*, present in *Allodesmus* (Berta and Wyss, 1994) and possibly incipient in *Desmatophoca* (Deméré and Berta, 2002).

Additional ambiguous synapomorphies of crown pinnipeds of Berta and Wyss (1994) include: enlarged tuberosities of the humerus, and a flattened and enlarged greater trochanter. A somewhat enlarged, though unflattened greater trochanter of the femur is observed in *Thalassoleon*. A somewhat enlarged lesser tubercle of the humerus that continues down the shaft as a cylindrical ridge, is observed in *Puijila*, *Semantor*, and the desmatophocids.

The earliest-diverging otariid (*Thalassoleon*) and phocid (*Devinophoca*) included in the analysis both display decidedly derived morphologies (Deméré and Berta, 2005; Koretsky et al., 2016). Yet, several character states previously believed to have been lost at the base of crown Pinnipedia are retained even in these taxa (Table 2). The earliest-diverging odobenid (Kohno, 1994; Boessenecker and Churchill, 2013) displays only a single purported pinniped synapomorphy of Berta and Wyss (1994)—presence of the antorbital process—a character which is now identified as an otarioid synapomorphy, and the specific configuration of this character in *Prototaria* is more appropriately considered an odobenid synapomorphy (Berta and Wyss, 1994). Deméré and Berta (2002) commented on the lack of the fovea for the teres femoris in *Proneotherium*, suggesting it would be expected given its transitional morphology. However, as this was offered as a pinniped synapomorphy, it should theoretically be present in *Proneotherium*. It would not be unexpected for a transitional odobenid to lack odobenid synapomorphies, but it would be unconceivable to observe a transitional odobenid lacking several pinniped synapomorphies, considering how few synapomorphies are identified (Berta and Wyss, 1994).

From the results of the present study, we reject many of the synapomorphies previously used to diagnose Pinnipedia, as many were founded on hypotheses of sister group relationships of Pinnipedia-Ursidae and Phocidae-Odobenidae. The present analysis recognizes a new suite of possible synapomorphies that support a monophyletic crown Pinnipedia, to the exclusion

**TABLE 3** | Synapomorphies of the clade Pinnipedia, as identified in the parsimony analysis of morphological data using TNT.

- 1. Fossa muscularis**
- 2. Nasals in dorsal view**
3. Premaxilla-nasal contact
4. Embayment for the inferior petrosal sinus
- 5. Auditory bullae, pseudoseptae**
6. P<sup>4</sup>, protocone
7. P/M relative size
8. P<sup>4</sup>, metastyle length
- 9. M<sup>1</sup>, metacone height**
10. M<sup>1</sup>, length of lingual half
11. M<sup>2</sup>, size
12. Humerus, supinator ridge extent/size
- 13. Humerus, greater tubercle extent/size**
14. Femur, ligamentum teres femoris presence
- 15. Femur, trochanteric fossa**

*Bolded characters are those that record >50% likelihood for the internode toward the base of Pinnipedia in the ACSR analysis employing maximum likelihood, as applied to the topology recovered from the Bayesian total-evidence tip-dating analysis.*

of *Puijila*, *Potamotherium*, *Enaliarctos*, and *Pteronarctos*. Admittedly, many of these possible synapomorphies cannot, at the present time, be identified in early-diverging members of the crown families due to inadequate preservation, and may turn out to represent independent derivations. Also, several of these synapomorphies require reversals to the ancestral condition in *Prototaria*, *Proneotherium*, *Thalassoleon*, and/or *Devinophoca* (synapomorphies 1, 3, 4, 6, 8, 10, 11, 12, 14 in **Table 3**), lessening the confidence with which we can assign them to the base of Pinnipedia. Furthermore, as with those identified by Berta and Wyss (1994), many of the synapomorphies identified here are uniquely approached by stem pinnipedimorphs, among arctoids. The stem pinnipedimorphs identified in the analysis appear to display a transitional or incipient state for many of these characters (synapomorphies 7, 8, 11, and 13 in **Table 3**), suggesting selective pressures favoring those traits were already present in stem pinnipedimorphs.

Thus, while the present analysis identifies a suite of potential pinniped synapomorphies, an investigation of their distribution among extinct taxa indicates that several of these features appear to be incipiently present in stem pinnipeds and others may have arisen in parallel among the three extant pinniped families. In the absence of incontestable transitional fossils, a more thorough investigation into the alpha and beta taxonomy of these known early-diverging taxa may provide additional clues regarding the divergence of otariids and phocids.

## Review of Parallel Evolution and Swimming Specialization in Arctoids

Swimming has evolved multiple times in arctoids (Berta et al., 2005). While no other known arctoids have developed the remarkable swimming specializations observed in pinnipedimorphs, many other taxa are considered to be semi-aquatic, including otters, the American mink, the European

mink, the polar bear, the robust otter-like fossil musteloid *Mionictis* (Baskin, 1998), and, if its affinities lie outside the pinniped divergence, *Kolponomos*. Otters, minks and *Mionictis* all share with *Puijila* and *Potamotherium* a similar ectomorph bodyplan and several other features related to swimming and aquatic feeding, including webbed digits (Savage, 1957; Berta et al., 2005; Rybczynski et al., 2009). These features are so numerous that they have even previously been used to assert the lutrine affinities of *Mionictis* (known from the middle Miocene) (Baskin, 1998; Tseng et al., 2009) and *Potamotherium*, though neither of these appear possible in the light of divergence time estimate studies consistently identifying a late Miocene divergence of Lutrinae (Sato et al., 2009). Considering these arctoid taxa converged upon similar specializations related to swimming, perhaps similar shifts could have begot flippers independently in otariids, phocids, and odobenids.

Adaptive radiations were thought to characterize the stem of pinnipedimorphs (Simpson, 1944), but recent evidence, based on tests of cranial disparity (Jones et al., 2015) and molecular markers (Higdon et al., 2007), suggest rapid radiations did not occur until the otarioid-phocoid split. Subsequent adaptive radiations appear to have taken place separately as otariids and odobenids diverged. This scenario is supported by the primitive morphologies of the early-diverging members of each extant pinniped family. Most notably, the early diverging odobenids *Prototaria* and *Proneotherium* do not depart significantly, in terms of morphology, from *Enaliarctos* and *Pteronarctos*. However, the results of the total-evidence tip-dating analysis indicate relatively rapid divergence events occurred along the stem, prior to a lull in identified speciations as the clades in crown Pinnipedia began to diverge. This high level of alpha and beta diversity is also reflected in the wide geographic distribution of stem pinnipeds.

Other molecular work has found evidence of genes that appear correlated with aquatic adaptation more broadly across marine mammals (Wang et al., 2008; Zhou et al., 2015), and of parallel shifts accelerating evolutionary rates of genes in multiple marine mammal clades (Chikina et al., 2016). However, convergent evolution of genes has been difficult to detect across marine mammal clades. Parallel substitutions of functionally-enriched genes do not appear to occur more frequently between marine mammals than they do between marine and terrestrial mammals (Irwin and Árnason, 1994; Foote et al., 2015; Zhou et al., 2015). While convergent molecular evolution and convergent phenotypic evolution are both common phenomena, adaptive molecular convergence associated with phenotypic convergence is uncommon (Foote et al., 2015).

Though our phylogenetic analyses identify a number of possible synapomorphies of crown pinnipeds, it is not possible to ascertain whether or not these shared traits arose via common ancestry or due to similar selective pressures on closely-related groups of organisms. Modern cladistics methods are not infallible. While more reliable than phenetic interpretations, phylogenetic inference of morphological data remains imprecise, and thus, susceptible to systematic error. This limits the confidence we can have in topological placements from such studies, including the present study.

The Mk model has monopolized Bayesian Inference of discrete morphological data. While it has been shown to be effective in simple data sets, it may not be able to accurately model morphological evolution. The Mk model employs a continuous-time Markov process running over finite state spaces (Klopfstein et al., 2015). A Markov process is conditioned only on the active state of the process. The past and future of the process are independent of the current state. Furthermore, the Markov process is also assumed to be at stationarity and time-reversible. A process attains stationarity when the current state ceases being dependent on the starting state. A process is time-reversible when its stochasticity does not become inconsistent or ill-defined if time is reversed.

The stationarity and time-reversibility of this Markov process prevents the Mk model from accounting for directional evolution (Klopfstein et al., 2015). Directional evolution, one of the three modes of selection originally proposed by Darwin (1859), involves an extreme phenotype being favored. Such selection is believed to be strong when an organism must adapt to a drastic and sudden shift in ecological pressures. Conceptually, directional selection would be a powerful propeller for an organism beginning to adapt to an aquatic existence. Conversely, in organisms that are secondarily aquatic, or highly specialized in some other manner, it should be unlikely, though not impossible, for organisms to revert to a less specialized form.

Since the Mk model does not allow for the input of assumptions of directional selection, it is unlikely that parallel evolution would reveal itself in a topology using the Mk model. A priori assumptions of directional selection are indeed difficult to integrate into an evolutionary model, but successful work has been carried out on characterizing directional selection in molecular datasets (Merritt and Quattro, 2001; Creevey and McInerney, 2004; Nielsen, 2005; Kosiol et al., 2008; McClellan, 2013; Enard et al., 2014; Bloom, 2017), allowing directional selection to be integrated into models of molecular evolution (Huelsenbeck et al., 2006; Ronquist et al., 2012b). Unfortunately, the non-objective nature of morphological characters and datasets, as outlined earlier in this chapter, makes it difficult to characterize directional selection as it relates to adaptive phenotypes. The extent of parallel evolution in pinnipeds may thus be greater than that suggested by the present study and others. It is possible that the extreme aquatic specializations characterizing extant pinnipeds, including flippers, developed in parallel in otariids, odobenids, and phocids, but our current phylogenetic methods are not capable of detecting such an event.

## CONCLUSION

Pinnipedimorpha, as currently defined, includes the most recent common ancestor of *Enaliarctos* and all of its descendents. The phylogenetic analyses of the present study provide support for the placement of additional fossil arctoid taxa at the base of this group. These “proto” pinnipeds come from disparate locations, deposits, and ages, and display a wide range of aquatic adaptations, ranging from the large-bodied molluscivore *Kolponomos* (Stirton, 1960), to the freshwater

otter-like forms *Puijila* and *Potamotherium*, to the aquatically-specialized *Semantor*. More detailed study of additional fossil arctoid taxa (including *Amphicticeps*), particularly with regards to their internal cranial architecture, may further explain the complexities associated with the transition of pinnipeds from a terrestrial to an aquatic environment.

At present, evidence overwhelmingly favors a monophyletic origin of pinnipeds. However, otariids, odobenids, and phocids display a startling amount of parallel evolution, as many of their shared features are absent in the early-diverging fossil ancestors of each family. Within a monophyletic framework, we postulate that parallel evolution may be the mechanism explaining their specialization within the aquatic realm, particularly with regards to raptorial feeding and hydrodynamic locomotion. A definitive answer awaits fossil evidence and the advancement of morphological phylogenetic methods. In the mean-time, statistical tests of convergence (Muschick et al., 2012; Ingram and Mahler, 2013; Arbuckle et al., 2014) could be applied to cladistic data sets of arctoids, to further examine the likelihood of parallel evolution within pinnipeds.

## DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in the **Appendix 3**.

## AUTHOR CONTRIBUTIONS

NR and NK conceived of the study. RP and NK collected data for the phylogenetic analysis. RP and HM ran the analyses. RP wrote the manuscript in consultation with NR, HM, and NK.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00457/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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