



Geometric morphometrics of macro- and meiofaunal priapulid pharyngeal teeth provides a proxy for studying Cambrian “tooth taxa”

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Abstract

Priapulids are marine, benthic ecdysozoan worms that feed using a distinctive toothed pharynx. While only a handful of lineages have survived to the present day, the Cambrian priapulid stem group left behind a rich record of articulated body fossils and characteristic trace fossils in the form of burrows. Recently, the fossil record of isolated priapulid cuticular elements including pharyngeal teeth has gained increased attention as a means of revealing cryptic priapulid taxa otherwise unknown among macrofossils. In this study, we focus on the ecological implications of shape variation in the teeth of extant and extinct priapulids, which display substantial morphological differences between taxa and life stages. We define a landmarking scheme to capture shape variation in priapulid teeth and apply it to our dataset, which includes a breadth of tooth specimens from extant macrofaunal and meiofaunal lineages alongside numerous Cambrian priapulid teeth preserved as isolated small carbonaceous fossils. Through ordination of the principal components of shape, we explore the priapulid tooth morphospace and find evidence that its occupancy has expanded since Cambrian times, indicating a corresponding expansion of the group’s ecological niche. We also employ our geometric morphometric approach to make linear discriminant analysis-based taxon assignments based on tooth morphology, which can be helpful for classifying enigmatic “tooth taxa” known solely from fossil teeth. Finally, we use discriminant analysis to study tooth shapes from a functional perspective, considering known ecologies to characterize the ecological functions of unclassified isolated teeth.

Keywords Priapulida · Cambrian · Meiofauna · Morphometrics · Ecology · Pharyngeal teeth

Introduction

Evolutionary conservation and innovation among priapulids

The fossil record indicates that total-group priapulids have been present in the world’s oceans since at least the Cambrian (Conway Morris 1977; Liu et al. 2014; Kesidis et al. 2019). Extant priapulids are represented by seven genera (Ahyong et al. 2023) distributed in five families (Fig. 1a) with uncertain interrelationships, two of which comprise macrofaunal taxa and the remaining three of which contain meiofaunal, poorly known clades. All families apart from the Priapulidae are monogeneric. The morphologically conserved priapulid bauplan (Fig. 1b and c) is rather simple, and consists of an anterior, muscular introvert (Fig. 1b, d, f) which houses a toothed, eversible pharynx (Fig. 1d, e) and is followed by an annulated trunk that commonly ends in one or more caudal appendages. The eversible pharynx

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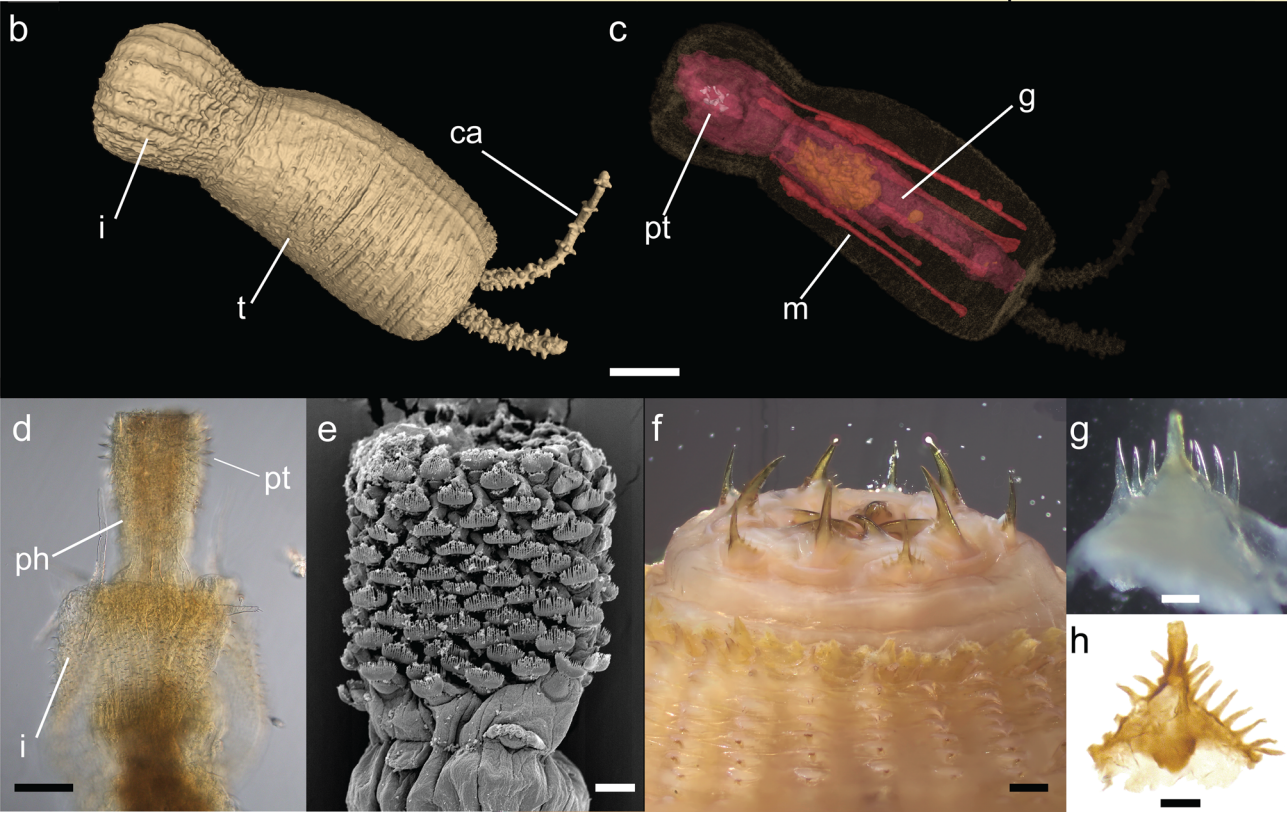
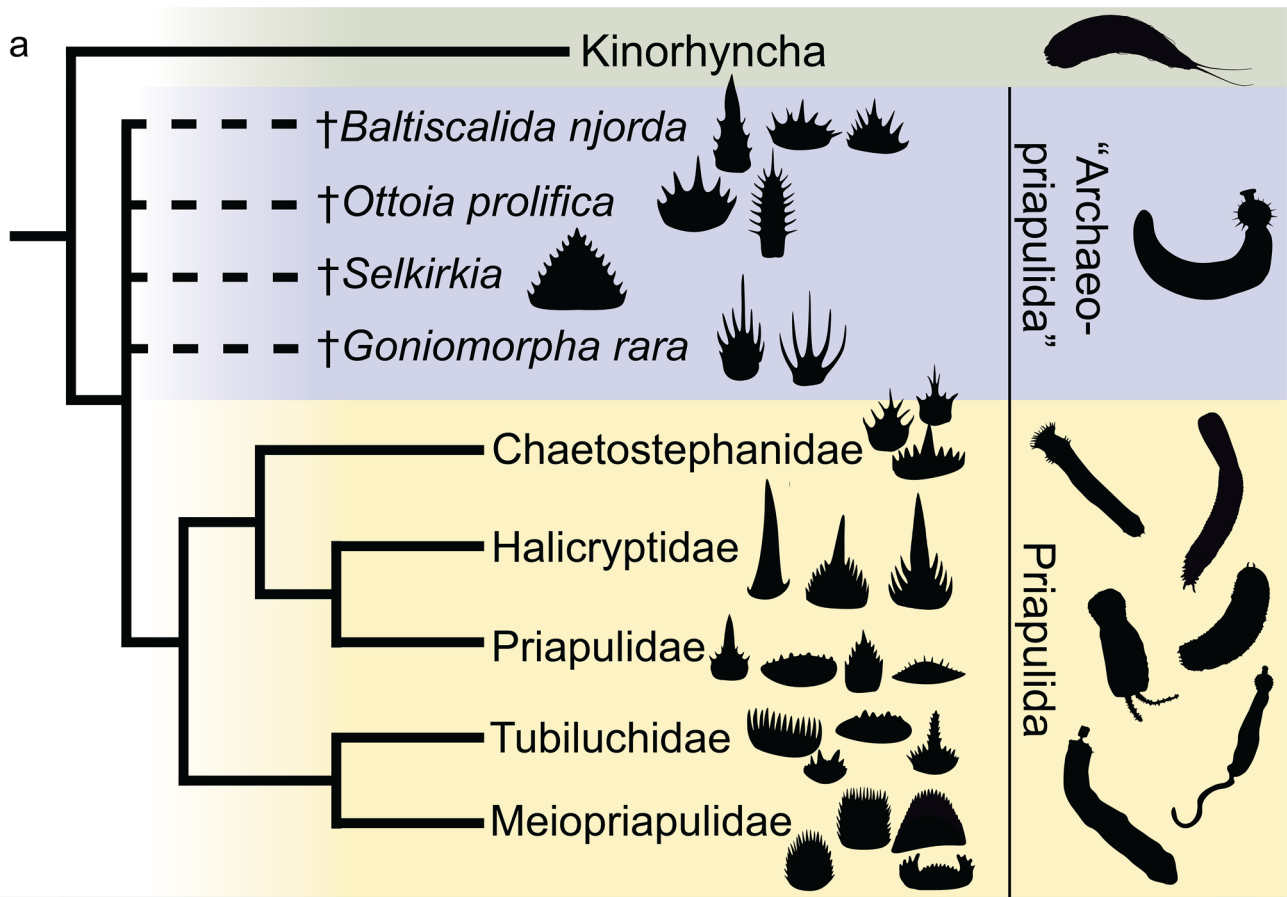


Fig. 1 **a** Priapulid phylogeny displaying main clades (see Schmidt-Rhaesa 2013), following the topology of Sansom (2016) with examples of tooth shapes. **b** Solid and **c** semi-transparent μ -CT 3D renderings of *Priapulopsis bicaudatus* (scale bar 100 μ m). **d** Introvert, everted pharynx and teeth of *Meiopriapululus* (scale bar 100 μ m). **e** Everted pharynx and teeth of *Tubiluchus* (scale bar 10 μ m). **f** Grasping apparatus with cuspidate teeth of *Halicryptus spinulosus*, TSZY-131 (scale bar 250 μ m). **g** Lower pharyngeal tooth of *Priapululus caudatus*, TSZY-106 (scale bar 100 μ m). **h** Early Cambrian priapulid tooth from Sweden preserved as an organic microfossil (scale bar 10 μ m). Abbreviations: introvert (i), trunk (t), caudal appendages (ca), pharyngeal teeth (pt), gut (g), introvert musculature (m), ph (pharynx)

and its associated teeth are instrumental in feeding, and the tooth shapes can vary substantially depending on the taxon and its feeding preferences. The pharyngeal teeth (Fig. 1g) can be broadly classified as fimbriated (finely fringed), pectinate (comb-like, Fig. 1e), or cuspidate (dagger-like, Fig. 1f). In terms of functional morphology, pectinate and fimbriated shapes seem to act as detrital rakes, brushes, or sieves (Kirsteuer and Rützler 1973; Calloway 1975; Storch et al. 1989), while cuspidate teeth are primarily of utility in holding on to struggling prey and preventing it from exiting the pharynx (Maas et al. 2007). In taxa that possess several types of teeth, the largest and the most cuspidate tend to be situated in the anterior-most tooth rings, with tooth size and degree of ‘cuspidity’ decreasing toward the posterior of the pharynx (see e.g., the descriptions in Shirley and Storch 1999; Storch et al. 1994). Macrofaunal priapulids, such as *Halicryptus* and *Priapululus*, are primarily predators on other invertebrates (van der Land 1970; Ankar and Sigvaldadottir 1981; Aarnio et al. 1998; Trott 1998; Huang et al. 2004a; Vannier 2012) and as adults have large, cuspidate teeth, while the meiofaunal lineages *Meiopriapululus* and *Tubiluchus* are primarily detritivorous (Kirsteuer and Rützler 1973; Calloway 1975; Morse 1981; Maas et al. 2007) and possess highly fimbriated and pectinate teeth. The temporal origins of meiofaunal priapulids are still unclear due to a lack of fossils, and although several miniscule total-group scalidophorans from the Cambrian are known (Dong et al. 2010; Liu et al. 2014, 2019; Shao et al. 2016; Zhang et al. 2018), they do not bear any specific resemblance to *Meiopriapulidae* or *Tubiluchidae*. Molecular clock data suggest that the extant meiofaunal priapulids may have diverged from other crown group priapulids already during the Palaeozoic era (Howard et al. 2022). Regardless, the miniaturization displayed among extant meiofaunal priapulid clades is an important morphological invention that sets them apart from other extant priapulids (Wills 1998; Wills et al. 2012), and which is likely coupled to their detritivorous lifestyles and derived tooth morphologies.

Cambrian priapulids and their record of isolated pharyngeal teeth

Despite playing a relatively inconspicuous role in the modern marine food web, priapulids appear to have had a prolific and widely distributed Cambrian stem group (Huang et al. 2004a, b; Vannier et al. 2010; Wills et al. 2012; Vannier 2012; Ma et al. 2014; Tian et al. 2015; Smith et al. 2015; Slater and Bohlin 2022). Priapulid-like animals of Cambrian age are often divided into two groups, both of which are likely paraphyletic: the palaeoscoleccids, with unclear relationships to extant priapulids, and the archaeopriapulids, which share a number of features with the priapulid crown group (Wills et al. 2012). Due to the closer relationship to extant priapulid taxa, we have herein chosen to focus on Cambrian taxa thought to belong to the ‘Archaeopriapulida’. Persistent scientific and public interest in the early evolution of animals has made some of the Cambrian stem group priapulids more familiar to a larger audience than most extant priapulid taxa, and the iconic genera *Ottoia* and *Selkirkia* from the Burgess Shale and other *konservat-Lagerstätten* are prominent examples. In addition to well-preserved body fossils and burrows, the record of Cambrian priapulids also comprises vast amounts of isolated pharyngeal teeth (Fig. 1h) preserved as organic microfossils (Butterfield and Harvey 2012; Smith et al. 2015; Slater et al. 2017; Slater and Bohlin 2022; Shan et al. 2022). Very little is known about the taxonomy and biology of these ‘tooth taxa’, and while *Ottoia* and *Selkirkia* are known from both body fossils and isolated teeth (Tian et al. 2015; Smith et al. 2015), the whole-organism morphology of taxa, such as *Baltiscalida* (Slater et al. 2017) and *Goniomorpha* (Shan et al. 2022), remain highly obscure, while numerous isolated teeth assigned to the form-taxon ‘*Ceratophyton*’ likely represent a mix of ancient stem-priapulids (Gravestock et al. 2001; Zang et al. 2007; Harvey et al. 2012; Kontorovich et al. 2012) as well as spines and fragments derived from other (non-priapulid) organisms. Analysis of shape variation in morphotaxa such as *Ceratophyton* may thus be helpful in testing its likely polyphyletic nature, but also in determining whether it is possible to delimit a genuine *Ceratophyton* sub-group that is distinct from other monophyletic taxa. In terms of diet, Cambrian taxa such as *Ottoia*, where gut contents are known, seem to have been rather generalist feeders that both ingested detritus and preyed on various other benthos (Vannier 2012), while *Selkirkia* leaned more toward detritivory (Tian et al. 2015). Naturally, nothing is yet known of dietary preferences for taxa known only from organic microfossils.

Geometric morphometrics as a way of studying priapulid tooth disparity and functions

We used geometric morphometrics (see Cooke and Terhune 2015 for an informative overview of the method) to

investigate the variation of pharyngeal tooth shapes in extant and Cambrian priapulids. Our findings support the notion that extant priapulids occupy a larger portion of the available morphospace compared to their ancient Cambrian counterparts. This observation may to some degree be influenced by the inclusion of extant meiofaunal taxa, whose putative Cambrian ancestors likely suffer from both a fossilization bias and detection issues. Although miniature Cambrian scolidophorans such as lorificerans are known to preserve (Harvey and Butterfield 2017), detection of such miniscule fossils remains difficult, and represents an additional challenge to the preservation barrier. In total, five extinct genera, plus a further group of isolated teeth of unknown origin were amenable to our analysis, and we found that linear discriminant analyses (LDA) was useful in assigning unclassified specimens of isolated Cambrian teeth to known/established taxa, and importantly, in distinguishing between tooth morphotypes adapted for detritivorous and carnivorous lifestyles.

Materials and methods

Data acquisition and literature review

We employed two-dimensional landmark-based geometric morphometrics to obtain shape variables for priapulid pharyngeal teeth. Our method involved capturing the widely disparate tooth shapes using a set of 19 topologically homologous landmarks, followed by Procrustes fitting. We then explored the priapulid tooth morphospace through principal components (PCA) and LDA analyses. This involved dissecting and photographing adult specimens of *Priapulus caudatus* and *Halicryptus spinulosus* from the collections of the Arctic University Museum of Norway under a ZEISS Discovery V12 stereo microscope (Supp. File 4). We also scoured the zoological and palaeontological literature for published photographs and graphic illustrations of priapulid pharyngeal teeth (Supp. File 1), including those from Cambrian taxa as well as larvae. We made every effort to include a broad range of tooth shapes from

various developmental stages of each taxon, and while most of the teeth studied herein are bilaterally symmetrical, some display varying degrees of asymmetry. To investigate the relationship between tooth shapes and their ecological roles, we conducted a literature review of dietary preferences to lay a foundation for specimen classification (Table 1). Our classification approach was based on the idea that evidence of predatory behavior in a given taxon should result in all the teeth possessed by members of that taxon being at least somewhat suited toward prey capture and classified as belonging to predatory morphotypes. Conversely, if a taxon is known to have a mostly detritivorous diet, all of its teeth would be classified as adapted for detritivory. Although this approach may be viewed as somewhat crude, we argue that it represents one of the few meaningful ways to glean information about an unknown animal's feeding ecology from isolated teeth.

Landmarking approach

We utilized the TpsUtil32 software to create a tps text file for our dataset, followed by landmark digitization in tpsDig2 v.2.3266 (Rohlf 2015), with 19 landmarks placed on each pharyngeal tooth (Fig. 2a). Use of the software's ruler function was avoided during the landmark placement process to preclude size-based biases on subsequent analyses, since our primary focus was on shape variation rather than size variation (which is an obvious parameter separating meio- and macrofaunal priapulids, and thus not of great interest). The points of maximum curvature at the bases and tips of the first, middle, and last three denticles on both sides of the central cusp or denticle were landmarked, with one landmark placed on the tip of the cusp or central denticle. Geometric morphometric analysis of characters in phylogenetically distant taxa can be challenging (Budd 2021), and the chosen landmarking locations almost certainly do not represent biologically homologous positions but are topologically homologous due to their placements at points of maximum curvature along the tooth's boundary (MacLeod 2013). This approach has the benefit of both being applicable to nearly

Table 1 Summary of taxon sampling and the knowledge status on feeding preferences

Clade	Feeding preferences
Halicryptidae	Primarily carnivorous, macrofauna and meiofauna (Ankar and Sigvaldadottir 1981; Aarnio et al. 1998)
Priapulidae	Primarily carnivorous, other invertebrates but also detritus (van der Land 1970; Trott 1998; Huang et al. 2004a; Vannier 2012), larvae are detritivores (van der Land 1970; Shirley 1990)
Chaetostephanidae	Largely unknown
Meiopriapulidae	Detritus, particles likely ingested by scraping (Morse 1981; Maas et al. 2007)
Tubiluchidae	Detritus, particles likely ingested by scraping (Kirsteuer and Rützler 1973; Calloway 1975)
“Archaeopriapulida”	Not well known, in <i>Ottoia</i> a diverse diet of invertebrates (Vannier 2012), in <i>Selkirkia</i> mostly detritus and likely small invertebrates (Tian et al. 2015)

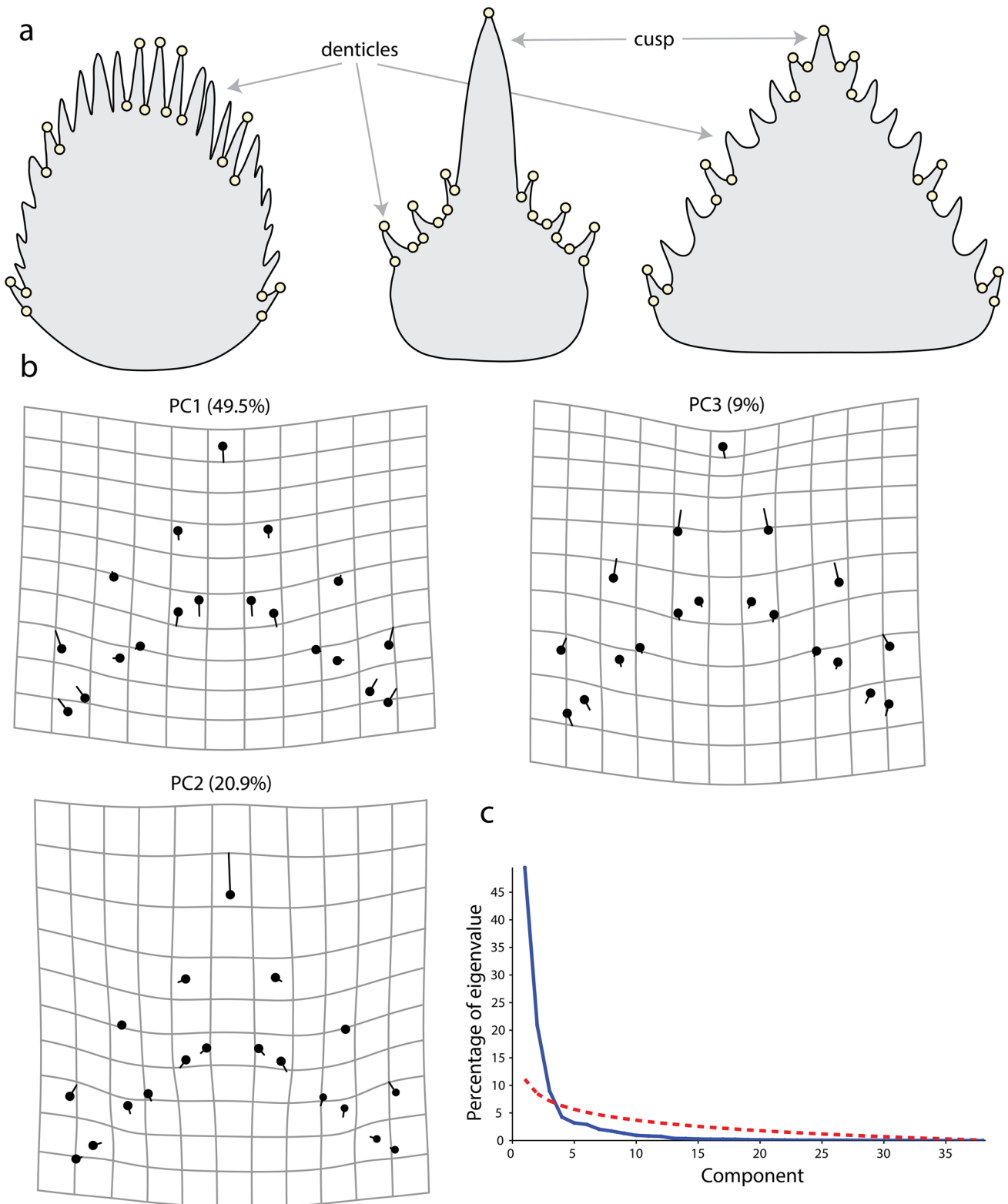


Fig. 2 **a** Overview of priapulid pharyngeal tooth morphology and explanations of the landmarking procedure as applied to different tooth shapes. The left tooth is of a fimbriated morphotype, while the middle tooth is cuspidate and the right tooth is pectinate. **b** Transfor-

mation grids of the first three principal components, which show the shape change compared to the mean shape as deformation of a rectangular grid. **c** Broken-stick scree plot illustrating the contribution of each principal component to the total variance of the dataset

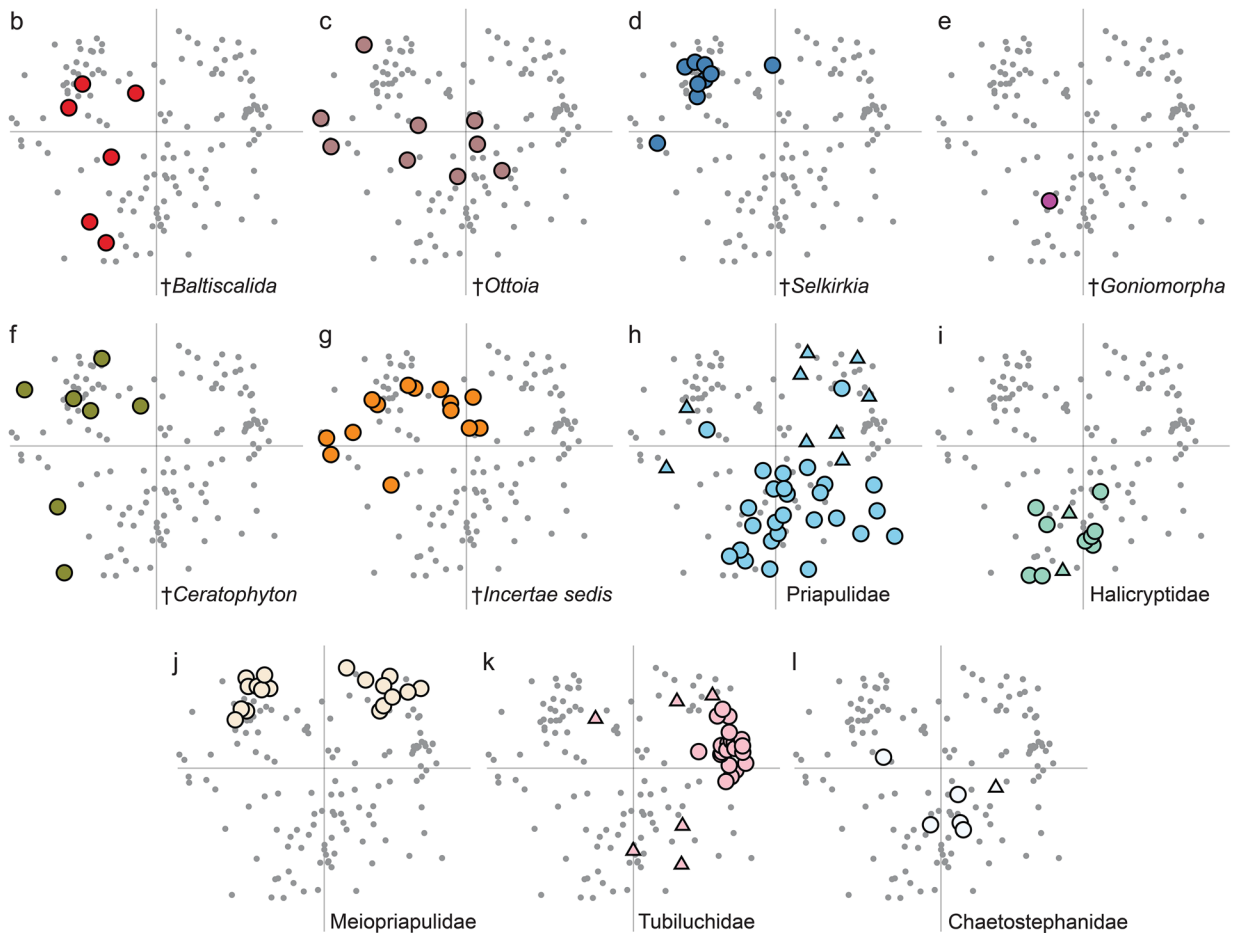
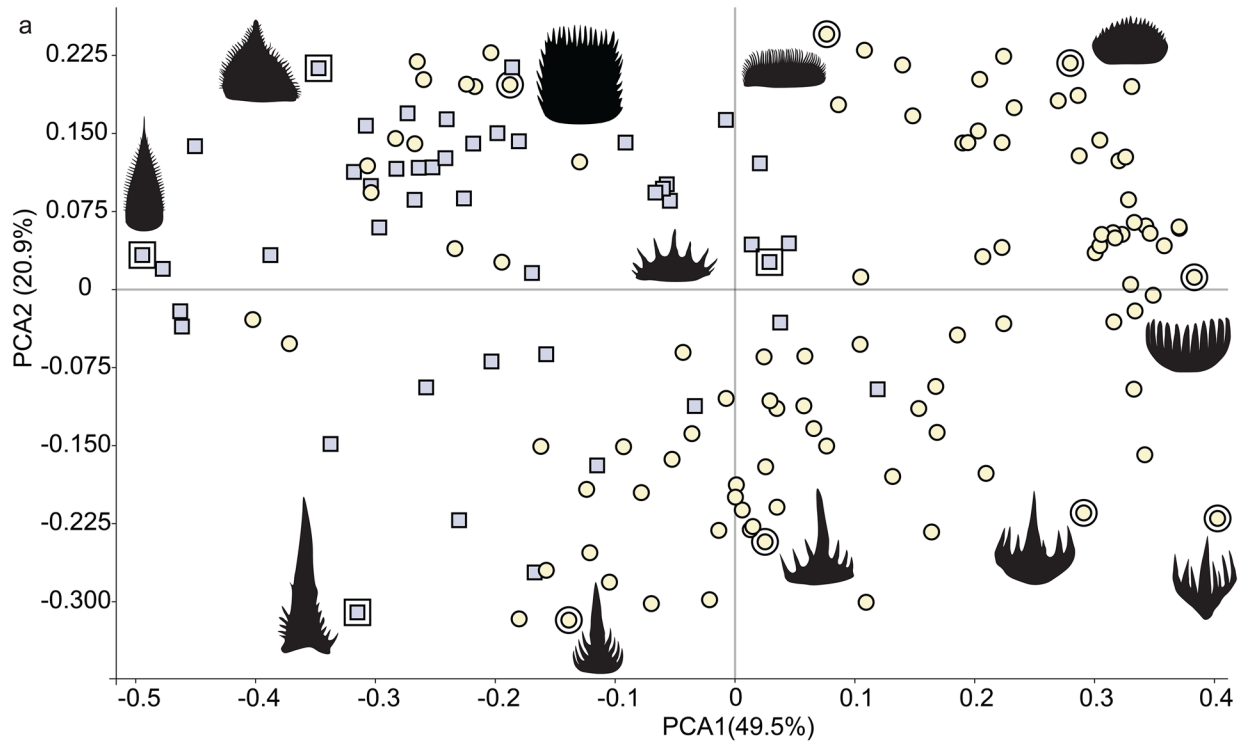


Fig. 3 a Multivariate morphospace for $n = 153$ specimens of priapulid pharyngeal teeth. Cambrian taxa are represented by boxes, extant taxa by circles. Outlines (not to scale) are displayed for select specimens, which are indicated by dilated symbols. **b–i** Positions of each studied fossil or extant taxon in the same morphospace. Triangles denote teeth from larval specimens

any tooth of extant and extinct priapulids and allowing for capture of relevant tooth geometry, e.g., of denticles and cusps (Fig. 2b). Despite the high applicability, some taxa with very divergent or simplified teeth, such as *Ottoia tricuspidata* (Smith et al. 2015) and *Eopriapulites sphinx* (Liu et al. 2014), could not be included in the analyses. Neither could various scalidophoran-like Cambrian fossils without well-preserved, morphologically distinct teeth (e.g., *Markuelia*; Dong et al. 2022) or which are known only from hook-shaped scalids (e.g., Slater et al. 2018). Apart from the high taxon diversity our approach permits, it also ensures efficiency of statistical computations and the prevention of some of the issues associated with sliding semi-landmark approaches (see MacLeod 2013 for further discussion on the topic). In cases where a bilaterally symmetrical tooth was damaged, mirroring of the intact side was performed, and slight breakages, skewing due to fossilization or obscured views due to the presence of debris, or low photographic resolution sometimes necessitated inferential placement of landmarks.

Multivariate analysis and ordination

Specimens were associated with information on taxon name, clade, geological age, size, life stage, and ecological information on dietary preferences (Supp. File 1) after which non-shape attributes of scale, orientation, and position were filtered from the landmark dataset by Procrustes fitting. Subsequently, shape variables were analyzed using PCA in MorphoJ (Klingenberg 2011), a method that reduces the dimensionality of multivariate datasets by reducing them to a set of uncorrelated axes (principal components) that together account for as much of the dataset's variance as possible. Further statistical analyses of the shape variables (Supp. File 2) were conducted in the software PAST 4.12 (Hammer et al. 2001). Linear discriminant analysis (also referred to as canonical variate analysis) is a method commonly used to classify specimens into predefined groups based on a set of continuous variables with the basic goal of finding a linear combination of variables that best explain the data, and was employed on the 10 first principal components to illustrate separation between groups and to attempt classification of specimens with unknown ecological functions. We subjected the linear discriminants to jackknife cross-validation (the benefits of which, compared to other cross-validation techniques, are described in Lance et al.

2000) to minimize bias in group assignments. To determine the extent to which larval-derived teeth influenced the analyses, we also ran PCA without larval specimens, and did not observe any substantial differences in the outcome. Teeth of larvae were therefore included in subsequent analyses.

Results

Despite the large diversity of tooth shapes covered, the morphospace of priapulid pharyngeal teeth (Fig. 3) illustrates reasonably distinct groupings of clades, with tooth specimens from closely related taxa generally clustering together. This finding is consistent with previous research that has noted the general stability of the priapulid morphospace across different sampled characters (Wills 1998; Wills et al. 2012).

Discriminant analysis-based inquiries of the first ten principal components (Fig. 4) into the link between tooth morphology and other variables including size, geological age, taxonomic identity, and inferred ecological function of the teeth demonstrated a clear separation between groups. Further supporting the separation between extant and Cambrian taxa observed in the PCA plot (Fig. 3), 82.19% of samples were correctly classified after jackknifing when discriminating by geological age (Fig. 4a). When discriminating by body size, the tooth shapes of larval and meiofaunal taxa appear to be distinct from those of macrofaunal, predatory priapulids (Fig. 4b) with 78.77% of samples correctly classified after jackknifing. Likewise, the discriminant analysis of feeding modes (Fig. 4c) achieved correct classification of 78.77% of samples after jackknifing, supporting the notable morphological differences between the teeth of detritivorous and predatory taxa (Fig. 4d). The attempt at classification of Cambrian-age teeth into their taxa was reasonably successful, with 50% of samples correctly classified after jackknifing (Fig. 4e).

Discussion

Dietary ecologies and ontogenetic patterns among extant priapulids

Extant priapulid taxa occupy most of the documented tooth morphospace (Fig. 3). Adult individuals of the macroscopic, predatory groups Priapulidae and Halicyptidae cluster in a distinct region of the morphospace, and the large coverages of their shape regions in the PCA plot are primarily driven by larval specimens with tooth morphologies partially different to those of adult animals. Likewise, the teeth of macroscopic and microscopic (meiofaunal and larvae of macrofaunal taxa) clades are distinct enough to form their

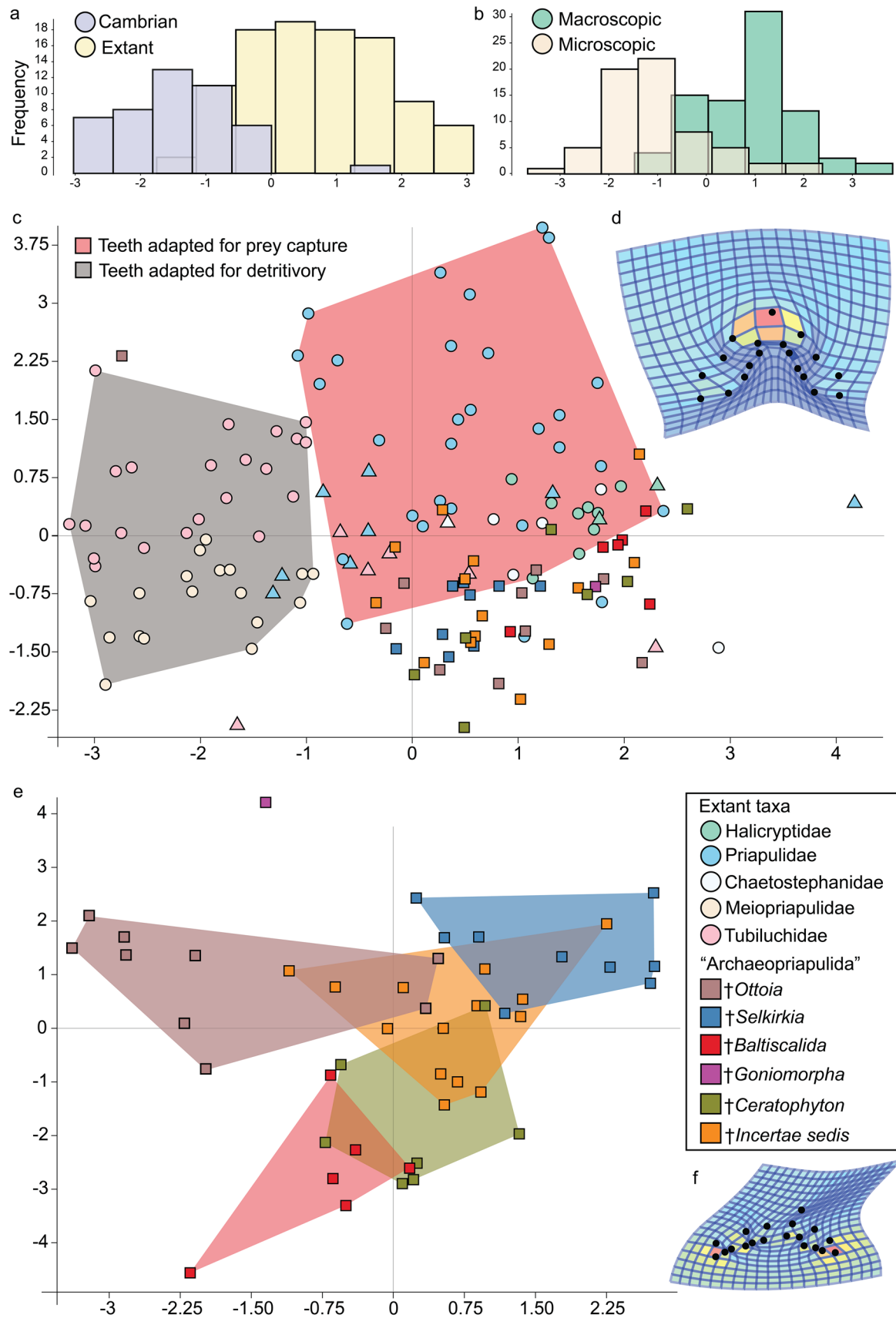


Fig. 4 Discriminant analysis plots of the first ten principal components of priapulid tooth shapes ($n=153$) as related to other variables. **a** Geological age. **b** Size (microscopic group including larvae of macrofaunal taxa) and **c** feeding mode Larval specimens are denoted by triangles. **d** Thin-plate spline deformation grid comparing a representative cuspidate and pectinate tooth. Colors indicate area expansion or contraction, and in this case demonstrate shape variation primarily around the cusp. **e** Classification of Cambrian taxa, where three unclassified specimens (orange) fall outside the shape variation of the other included taxa. **f** Deformation grid comparing the mean “archaeopriapulid” tooth shape to that of the possibly distorted specimen of *Goniomorpha*

own regions in the shape space and to be well separated using LDA (Fig. 4b), an expected outcome given the known differences in feeding ecologies between microscopic and macroscopic priapulids (Table 1). We also identified striking shape similarity in tooth shapes between teeth of larval Priapulidae and the meiofaunal, detritivorous lineages Tubiluchidae and Meiopriapulidae (Figs. 3, 4c). Larvae of *Priapululus caudatus* are known to be primarily detritivorous (van der Land 1970; Kirsteuer and Rützler 1973; Shirley 1990), but have been thought to ingest sediments primarily using their cuspidate teeth (Kirsteuer and Rützler 1973). We find it likely, based on our results, that the more pectinate teeth of larval Priapulidae in fact also have an important function in raking and brushing sediments into the mouth and pharynx. This observation may reflect either a case of evolutionary convergence of teeth in larval Priapulidae and the meiofaunal groups or that evolution by heterochrony/retention of larval traits was an important factor in the emergence of meiofaunal forms. Chaetostephanidae, the third group of miniaturized priapulids which contains only the genus *Maccabeus*, appears to have tooth shapes more similar to predatory taxa (Figs. 3a, 4c). As *Maccabeus* is arguably the rarest and most obscure member of the living priapulid taxa, this potential insight into its ecology could be of high interest to future priapulid ecologists.

Cambrian priapulids occupy a limited region of the documented tooth morphospace

Our investigation into priapulid tooth shapes reveals that extant and Cambrian priapulid teeth occupy somewhat different parts of the shape space (Fig. 3) and suggests that extant taxa have evolved a greater diversity of tooth shapes than their Cambrian counterparts. Teeth of extant and Cambrian priapulids are also distinct enough to be well separated by LDA (Fig. 4a), although this separation is likely driven partially by the inclusion of meiofaunal and larval specimens in the extant group. These findings challenge the prevailing notion of priapulids as evolutionary stagnant ‘living fossils’, and supports indications of a post-Cambrian expansion of the priapulid morphospace (Wills 1998; Wills et al. 2012). Interestingly, extant taxa are not represented in some regions

of the shape space, which are instead defined by Cambrian priapulids (Fig. 3) indicating that some Cambrian tooth shapes have vanished, perhaps due to changes in dietary ecologies or the oceanic ecosystem at large. Nonetheless, it is important to note that the fossil record may be biased due to the rarity of preserved miniscule or meiofaunal forms and larvae. While the true diversity of Palaeozoic priapulids therefore remains an “unknown unknown”, many fossilized scalidophorans in the size range occupied by *Tubiluchus* and *Meiopriapululus* are known (Dong et al. 2010; Liu et al. 2014, 2019; Shao et al. 2016; Zhang et al. 2018; Peel 2022). It is also possible that some pharyngeal teeth preserved as carbonaceous microfossils have not yet been identified as such due to highly derived or simplified morphologies. Phylogenetic placement of these fossils is not a trivial task, but hitherto they have not been considered affiliated with extant meiofaunal priapulids, and they do not display tooth morphologies similar to those of Tubiluchidae or Meiopriapulidae. As a way to address the issues of preservation and detection, further exploration of the record of organic microfossils may yield insights into early priapulids that are otherwise missing from the fossil record (Butterfield and Harvey 2012; Slater et al. 2017; Slater and Bohlin 2022). Additionally, the topic of symmetry in the teeth of both extant and Cambrian priapulids may be an interesting future avenue of research.

Discriminant analysis as a tool for taxon- and ecology assignments of isolated teeth

The landmarking and geometric morphometric analysis approach proved to be an effective method for capturing tooth morphology in enough detail to carry reasonably strong ecological and phylogenetic signals, as demonstrated by our discriminant analyses (Fig. 4). The LDA and classification of tooth functional morphology (Fig. 4c) indicates that the tooth shapes of Cambrian taxa are most similar to those of the extant macroscopic and predatory groups Halicyrtidae and Priapulidae. While this observation is unsurprising for Cambrian genera with well-documented predatory lifestyles, such as *Ottoia* (Vannier 2012), the teeth of the suspected detritivore *Selkirkia* (Tian et al. 2015) remained mostly unclassified in the LDA and are not found to be particularly similar to those of extant detritivorous clades. Similarly, the “tooth taxa” *Baltiscalida* and *Goniomorpha* in addition to the form-taxon *Ceratophyton* and *Incertae sedis* specimens remain mostly unclassified, but generally form a cluster close to the teeth defined as adapted for predation. Our LDA of Cambrian taxa (Fig. 4e) indicates that certain unidentified specimens in the *Incertae sedis* group are likely to be unassigned *Baltiscalida*, *Selkirkia* and *Ottoia*, as they show a high degree of shape similarity to those taxa. This observation is also true for some specimens that belong to the waste-basket taxon *Ceratophyton*, which lends further

support to its suspected polyphyletic nature. Additionally, the LDA analysis clearly separated the single specimen of *Goniomorpha* included in our dataset from the other “archaeopriapulid” taxa (Fig. 4e). Whether this is due to genuinely aberrant morphology in *Goniomorpha* or the fact that the specimen seems taphonomically distorted to some degree (Fig. 4f) will remain unclear until more specimens become available for analysis. These findings may be of particular use for paleontologists working with taxonomy of small carbonaceous fossils, allowing for accurate classification of unclassified specimens. Further, we have provided a more objective way of assessing the relationship between tooth morphotypes and diet than informed guesswork alone (Fig. 4e). While this approach relies on a somewhat rudimentary theoretical foundation, we argue that further research into the functional morphology of priapulid teeth and a refined knowledge of dietary habits will enhance its usefulness in predicting the ecologies of fossil “tooth taxa”.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00435-023-00617-4>.

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Author contributions JWV conceived of the study, collected data, performed analyses, and drafted the manuscript and figures. DC contributed to the geometric morphometric study design. AA, BJS, & MVS also contributed to study design, data acquisition, and manuscript writing. All authors contributed to, and approved of, the final version of the manuscript.

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Data availability The authors confirm that all relevant data generated in this study are contained in the article and/or its supplementary information files.

Declarations

Conflict of interest The authors have no competing interests to declare.

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