Organisms Diversity & Evolution
https://doi.org/10.1007/s13127-021-00482-3

ORIGINAL ARTICLE

Untangling the diversity and evolution of tentacles in scallops, oysters, and their relatives (Bivalvia: Pteriomorphia)

Jorge A. Audino[1] · **Jeanne M. Serb**[2] · **José Eduardo A. R. Marian**[1]

Received: 9 September 2020 / Accepted: 3 January 2021

Abstract

Tentacles are fascinating, multifunctional organs found in many aquatic invertebrate groups. In bivalves, tentacles are morphologically diverse, performing protective and sensory roles in taxa from different ecological niches. Such diversity is particularly accentuated in Pteriomorphia, a clade comprising scallops, oysters, file clams, and relatives. However, little is known about the evolution of these organs and their role in bivalve radiation. To test hypotheses of convergent tentacular evolution and a possible association between tentacles and body orientation on the substrate, we first examined tentacle morphology in 108 preserved species representing 15 families across Pteriomorphia. Morphological descriptions of tentacle type (inner mantle fold tentacles, IFT; middle mantle fold tentacles, MFT) and position (marginal and submarginal) are provided, expanding the knowledge of less studied bivalve taxa. Then, we placed the morphological dataset under a molecular phylogenetic framework to estimate ancestral states. IFT had likely four independent origins, while MFT emerged twice independently. After being gained, tentacles have not been lost. In addition, evolution of MFT coincides with transitions in body position with the midsagittal plane parallel to the substrate in the clades of scallops (Pectinida) and oysters (Ostreida). Such a shift could be related to the increase of mantle exposure, favoring the emergence of serially repeated organs, such as tentacles. Altogether, our results support the convergent evolution of tentacles across different taxonomic levels, corroborating the plasticity of the molluscan body and the relevance of evolutionary convergences in the radiation of bivalves.

Keywords Bivalves · Evolutionary convergence · Mollusca · Morphology · Phylogeny · Sensory

Introduction

Morphological innovations and convergent evolution are frequently associated with evolutionary radiations and broad-scale patterns of biological diversity (Schluter 2000; Mahler et al. 2017). In this context, tentacular organs represent a valuable source of data to investigate phenotypic evolution and adaptive innovations because of their morphological and functional diversity (e.g., Roberts and Moore 1997; Pellmyr and Krenn 2002; Kier 2016; Kuzmina and Temereva 2019). Tentacles are elongate, flexible processes—more prominent than small, rounded papillae—that function as muscular hydrostats (Carter et al. 2012). Tentacles occur in many invertebrate groups, which use these organs for a variety of functions. Some examples include prey capture and manipulation of food particles, as observed in cnidarians, bryozoans, and polychaetes (Dubois et al. 2005; Shimizu and Namikawa 2009). Tentacles can also display defensive roles, including chemical defense in file clams (Dougherty et al. 2019) and autotomy in medusae (Bickell-Page and Mackie 1991). In many invertebrate groups, tentacles are specialized organs used to sense the environment by detecting olfactory and tactile stimuli (Künz and Haszprunar 2001; Ruth et al. 2002). While some of these appendages have been extensively investigated in mollusks, such as the cephalic tentacles of gastropods (e.g., Haszprunar et al. 2017), comparative data are still

✉ Jorge A. Audino
jorgeaudino@ib.usp.br

Jeanne M. Serb
serb@iastate.edu

José Eduardo A. R. Marian
jemarian@ib.usp.br

[1] Department of Zoology, University of São Paulo, Rua do Matão, Travessa 14, n. 101, São Paulo, São Paulo 05508-090, Brazil

[2] Department of Ecology, Evolution and Organismal Biology, Iowa State University, 2200 Osborn Dr., Ames, IA 50011, USA

required to characterize morphological and functional diversity and unravel the evolutionary history of tentacular structures.

In molluscan bivalves, tentacles are common and diverse anatomical structures (Yonge 1983) (Fig. 1) that occur along the mantle margin, i.e., the free extension of the mantle, lining the shell edge (Carter et al. 2012). Varying from few, slender projections in some anomalodesmatan bivalves (Machado et al. 2017) to numerous, enormous organs in file clams (Mikkelsen and Bieler 2003), tentacles may occur on the inner and middle folds of the mantle margin (Fig. 1a–e) (Yonge 1983). In bivalves that live buried in the substrate (infaunal), tentacles are commonly found at the tip or lining the inner walls of siphons to protect the incurrent and excurrent apertures from large sediment particles (Hodgson and Fielden 1984; Fishelson 2000; Sartori et al. 2008; Vitonis et al. 2012). In bivalves living above the substrate (epifaunal), tentacles are also present, being particularly large and abundant among pteriomorphians. The Pteriomorphia is a large clade comprised by 26 families (MolluscaBase 2020; Bieler et al. 2010) and includes many tentaculate groups, such us the scallops and relatives (Pectinoidea), file clams (Limoidea), pen shells (Pinnoidea), pearl oysters and relatives (Pterioidea), and oysters (Ostreoidea). Interestingly, tentacles share some gross similarities across pteriomorphian lineages, including location at the mantle margin, abundance and distribution along the margin, and slender morphology. In functional terms, tentacles are supposed to be sensory organs, also acting as secretory and protective structures in oysters, scallops, and file clams (Gilmour 1967; Waller 1976; Moir 1977; Audino et al. 2015; Audino and Marian 2020).

Despite the existing morphological information for selected taxa, tentacle evolution is still poorly known for epifaunal bivalves, and hypotheses of trait evolution are conflicting. In a previous attempt to examine tentacle evolution in pteriomorphians, Waller (1978) focused on their position, ability to extend, and functional specialization. He hypothesized that “generalized” tentacles (assigned to Pterioidea) would have originated more “specialized” organs, with a common origin of extensible tentacles between Ostreoidea and Pectinoidea (Waller 1978). Conversely, a later morphological and phylogenetic investigation has suggested that tentacles on the middle mantle fold of Pterioidea and Ostreoidea are homologous (Tëmkin 2006), i.e., share a common, phylogenetic origin. Detailed anatomy seems to support this hypothesis, due to similarities in cilia distribution and innervation between the tentacles of these two clades (Audino and Marian 2020). However, in a broader taxonomic context, detailed anatomical data suggests that tentacles might not have a single, common origin in Pteriomorphia, possibly including independent acquisitions in scallops and relatives (Pectinoidea) (Audino and Marian 2020). To test the hypothesis that tentacles represent evolutionary convergences, i.e., similar phenotypes with independent evolution (Agrawal 2017), comparative morphological study within the phylogenetic framework of Pteriomorphia is necessary.

Ecological factors, such as substrate occupation and lifestyles, may also contribute to the tentacle diversification. It has been shown that body position relative to substrate has had a critical influence on shell shape, substrate occupation, and lifestyle evolution in pteriomorphian bivalves (Kauffman 1969; Stanley 1972; Seilacher 1984; Harper and Skelton 1993; Sherratt et al. 2016). For instance, the orientation of the midsagittal plane (Fig. 2a, b), i.e., which divides the body in left and right halves (Carter et al. 2012), defines the position for physical stabilization and which part of the body reclines on the substrate. In epifaunal bivalves, attachment using a tuft of proteinaceous filaments (i.e., byssus) is ventral, so the midsagittal plane is perpendicular to the substrate (Fig. 2c), resulting in both valves supporting the body (Stanley 1972), a condition observed in mussels (Mytilidae). In contrast, only

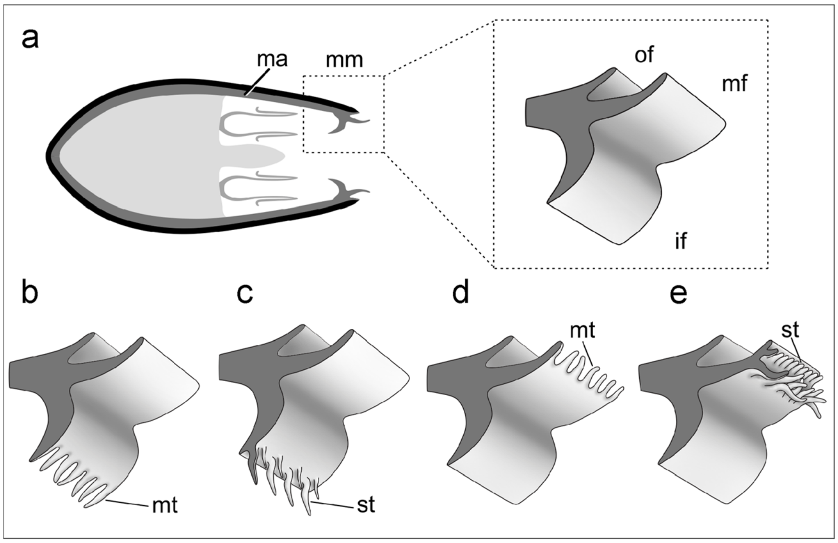

Fig. 1 Schematic representations of tentacle position on the mantle margin of pteriomorphian bivalves. Inner fold tentacles (IFT) in **b** and **c**, middle fold tentacles (MFT) in **d** and **e**. **a** Transverse section through the bivalve body with the mantle margin exposed, illustrating the mantle folds devoid of tentacles (inset). **b** Marginal IFT. **c** Submarginal IFT. **d** Marginal MFT. **e** Submarginal MFT. if, inner mantle fold; ma, mantle; mf, middle mantle fold; mm, mantle margin; mt, marginal tentacles; of, outer mantle fold; st, submarginal tentacles

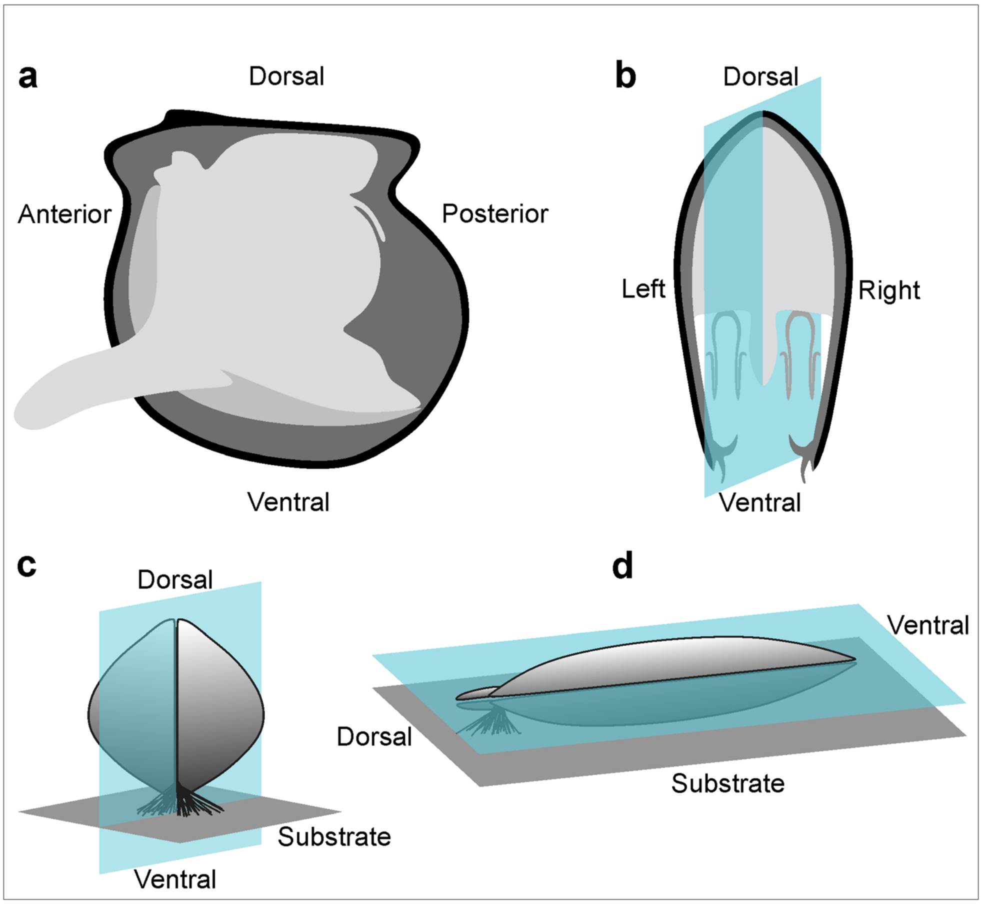

Fig. 2 Schematic representations of bivalve body axes and position relative to substrate. The midsagittal plane, i.e., dividing the body in two halves (left and right), is represented by translucent rectangles. Lateral view in **a** and anterior view in **b**–**d**. **a** Lateral view of the left side of the bivalve body after removal of the left valve. **b** Transverse section through the bivalve body. **c** Midsagittal plane perpendicular to the substrate. **d** Midsagittal plane nearly parallel to the substrate

one valve supports the body in scallops (Pectinidae), in which the midsagittal plane is at a low angle (parallel) to the substrate (Fig. 2d) (Stanley 1972). This latter condition was hypothesized to be associated with an enlargement of the mantle margin, increasing its surface area and exposure to the environment, which could support the development of repeated sensory receptors (Kauffman 1969). In this context, we expect tentacles to have evolved as repeated sensory organs in pteriomorphian lineages that adopted a parallel position of the midsagittal plane on the substrate. The Pteriomorphia is a suitable model to explore this hypothesis of association between lifestyle and tentacle evolution for two reasons. First, the clade includes both tentacled and tentacle-less species. Second, the midsagittal plane is perpendicular to the substrate in some epifaunal lineages, while it is parallel in others.

Considering the functional and morphological diversity of tentacles in pteriomorphians, these organs are valuable to gain insights into phenotypic evolution and adaptation in bivalves. Therefore, we have analyzed the morphology of tentacles of preserved species across Pteriomorphia and placed this dataset under a phylogenetic framework to (1) assess tentacle diversity across pteriomorphian taxa, (2) test whether tentacles are convergent and infer how many times they have evolved, and (3) investigate if tentacle evolution is associated with body position relative to the substrate.

Material and methods

Taxa sampling

Mantle tentacles were investigated for location, distribution, shape, relative size, and position over the mantle fold in 108 species from 15 families of Pteriomorphia (Table 1). Representatives of mussels (Mytilidae) and ark clams and relatives (Arcoidea and Limopsoidea) were not investigated herein due to the well-known absence of tentacles on their mantle margin, as previously reported in many morphological studies (e.g., Soot-Ryen 1955; Waller 1980; Morton and Peharda 2008; Audino and Marian 2018; Audino et al. 2020a). Preserved specimens were examined in ethanol under stereomicroscopes provided by the respective museum facilities and photographed by a smartphone camera (Apple iPhone 5s, 8 megapixels) coupled to the ocular lens. Catalog numbers are listed in Table 1 for the following collections: Museum of Comparative Zoology (MCZ), Museum of Zoology “Prof.

Table 1 Bivalve taxa investigated, respective catalog numbers and collections, and summary of the survey on tentacle presence and position

Taxa	Catalog number	IFT	MFT
Anomiidae Rafinesque, 1815			
Anomia simplex d'Orbigny, 1853	ZUECBIV1423, USNM804291, USNM804325, MCZ280425	–	Submarginal
Heteranomia squamula (Linnaeus, 1758)	USNM871362, MCZ300656	–	Submarginal
Pododesmus macrochisma (Deshayes, 1839)	SBMNH361457	–	Submarginal
Pododesmus rudis (Broderip, 1834)	USNM850821, USNM847837	–	Submarginal
Dimyidae Fischer, 1886			
Dimya argentea Dall, 1886	USNM855224	–	Submarginal
Gryphaeidae Vyalov, 1936			
Hyotissa hyotis (Linnaeus, 1758)	MCZ378999	Marginal	Submarginal
Hyotissa mcgintyi (Harry, 1985)	MZSP118279, USNM804282	Marginal	Submarginal
Hyotissa numisma (Lamarck, 1819)	USNM803328	Marginal	Submarginal
Hyotissa sinensis (Gmelin, 1791)	SBMNH141713	Marginal	Submarginal
Neopicnodonte cochlear (Poli, 1795)	MCZ379076	Marginal	Submarginal
Isognomonidae Woodring, 1925 (1828)			
Isognomon alatus (Gmelin, 1791)	MZSP89628, USNM836243	Marginal	Marginal
Isognomon bicolor (Adams, 1845)	ZUECBIV2123	Marginal	Marginal
Isognomon ephippium (Linnaeus, 1758)	USNM701010	Marginal	Marginal
Isognomon isognomum (Linnaeus, 1758)	MZSP54988	Marginal	Marginal
Isognomon perna (Linnaeus, 1767)	MZSP71186, MZSP11583	Marginal	Marginal
Isognomon radiatus (Anton, 1838)	USNM803357	Marginal	Marginal
Limidae d'Orbigny, 1846			
Acesta mori (Hertlein, 1952)	MCZ384449	–	Submarginal
Acesta oophaga Järnegren, Schander and Young, 2007	USNM1263635	–	Submarginal
Acesta sphoni (Hertlein, 1963)	SBMNH424265	–	Submarginal
Ctenoides mitis (Lamarck, 1807)	USNM664306, MCZ378941	–	Submarginal
Ctenoides scaber (Born, 1778)	USNM833716, MCZ376728	–	Submarginal
Lima lima (Linnaeus, 1758)	USNM754383	–	Submarginal
Limaria fragilis (Gmelin, 1791)	USNM700291, USNM78784	–	Submarginal
Limaria hians (Gmelin, 1791)	MCZ371725	–	Submarginal
Limaria orbignyi (Lamy, 1930)	SBMNH19892	–	Submarginal
Limaria pellucida (C. B. Adams, 1848)	ZUECBIV2130, USNM850805	–	Submarginal
Limatula celtica J. A. Allen, 2004	MCZ357556	–	Submarginal
Limatula hodgsoni (E. A. Smith, 1907)	USNM882395	–	Submarginal
Limatula setifera Dall, 1886	USNM850807	–	Submarginal
Limatula subovata (Monterosato, 1875)	ZUECBIV5733, MCZ357577	–	Submarginal
Limea pygmaea (Philippi, 1845)	ZUECBIV2207	–	Submarginal
Malleidae Lamarck, 1818			
Malleus albus Lamarck, 1819	MZSP55595	Marginal	Marginal
Malleus candeanus (d'Orbigny, 1853)	USNM847920, MCZ340681	Marginal	Marginal
Malleus malleus (Linnaeus, 1758)	USNM802338	Marginal	Marginal
Malleus regula (Forsskål in Niebuhr, 1775)	MCZ379030	Marginal	Marginal
Margaritidae Blainville, 1824			
Pinctada albina (Lamarck, 1819)	USNM755664	Marginal	Marginal
Pinctada imbricata Röding, 1798	ZUECBIV2383	Marginal	Marginal
Pinctada maculata (Gould, 1850)	USNM801689	Marginal	Marginal
Pinctada margaritifera (Linnaeus, 1758)	USNM836493	Marginal	Marginal
Pinctada mazatlanica (Hanley, 1856)	SBMNH42703	Marginal	Marginal
Pinctada radiata (Leach, 1814)	MZSP106549	Marginal	Marginal
Ostreidae Rafinesque, 1815			
Crassostrea gigas (Thunerg, 1793)	USNM836263	Marginal	Submarginal
Crassostrea virginica (Gmelin, 1791)	USNM804279	Marginal	Submarginal
Dendostrea folium (Linnaeus, 1758)	USNM802346	Marginal	Submarginal
Dendostrea frons (Linnaeus, 1758)	USNM804288, MCZ378951	Marginal	Submarginal
Lopha cristagalli (Linnaeus, 1758)	USNM793723	Marginal	Submarginal
Ostrea edulis Linnaeus, 1758	USNM836256, MCZ379114	Marginal	Submarginal

Table 1 (continued)

Taxa	Catalog number	IFT	MFT
Ostrea equestris Say, 1834	USNM801030	Marginal	Submarginal
Ostrea permollis G. B. Sowerby II, 1871	USNM850800	Marginal	Submarginal
Pustulostrea australis (Lamarck, 1819)	USNM787959	Marginal	Submarginal
Saccostrea cucullata (Born, 1778)	SBMNH345722	Marginal	Submarginal
Saccostrea palmula (Carpenter, 1857)	USNM796192	Marginal	Submarginal
Striostrea prismatica (Gray, 1825)	SBMNH212884	Marginal	Submarginal
Pectinidae Rafinesque, 1815			
Adamussium colbecki (E. A. Smith, 1902)	USNM886965	Submarginal	Submarginal
Aequipecten glyptus (A. E. Verrill, 1882)	USNM803317	Submarginal	Submarginal
Aequipecten muscosus (W. Wood, 1828)	USNM855448	Submarginal	Submarginal
Aequipecten opercularis (Linnaeus, 1758)	MCZ371755	Submarginal	Submarginal
Amusium sp.	USNM804083	Submarginal	Submarginal
Argopecten gibbus (Linnaeus, 1758)	USNM801015, MCZ319455	Submarginal	Submarginal
Argopecten irradians (Lamarck, 1819)	MCZ278251	Submarginal	Submarginal
Chlamys hastata (G. B. Sowerby II, 1842)	USNM739716	Submarginal	Submarginal
Chlamys islandica (Müller, 1776)	MCZ319213	Submarginal	Submarginal
Crassadoma gigantea (Gray, 1825)	SBMNH466682	Submarginal	Submarginal
Delectopecten vitreus (Gmelin, 1791)	USNM757159	Submarginal	Submarginal
Euvola raveneli (Dall, 1898)	USNM801009	Submarginal	Submarginal
Euvola ziczac (Linnaeus, 1758)	USNM833726	Submarginal	Submarginal
Flexopecten glaber (Linnaeus, 1758)	MCZ371469	Submarginal	Submarginal
Gloripallium pallium (Linnaeus, 1758)	USNM701201	Submarginal	Submarginal
Mimachlamys munda (Reeve, 1853)	USNM855527, USNM855529	Submarginal	Submarginal
Mimachlamys varia (Linnaeus, 1758)	MCZ378918	Submarginal	Submarginal
Mirapecten mirificus (Reeve, 1853)	USNM886347	Submarginal	Submarginal
Palliolum tigerinum (O. F. Müller, 1776)	MCZ376695	Submarginal	Submarginal
Pecten jacobaeus (Linnaeus, 1758)	USNM1086023	Submarginal	Submarginal
Pedum spondyloideum (Gmelin, 1791)	USNM793736	Submarginal	Submarginal
Placopecten magellanicus (Gmelin, 1791)	USNM829091, MCZ319444	Submarginal	Submarginal
Spathochlamys benedicti (Verrill and Bush [in Verrill], 1897)	USNM804647	Submarginal	Submarginal
Zygochlamys patagonica (P. P. King, 1832)	USNM886527	Submarginal	Submarginal
Pinnidae Leach, 1819			
Atrina inflata (Dillwyn, 1817)	MZSP55029	Marginal	–
Atrina maura (G. B. Sowerby I, 1835)	USNM828614	Marginal	–
Atrina rigida (Lightfoot, 1786)	USNM847971	Marginal	–
Atrina seminuda (Lamarck, 1819)	ZUECBIV2135	Marginal	–
Atrina serrata (G. B. Sowerby I, 1825)	USNM801651	Marginal	–
Atrina vexillum (Born, 1778)	USNM793718	Marginal	–
Pinna carnea Gmelin, 1791	MZSP29040, USNM804284	Marginal	–
Pinna muricata (Linnaeus, 1758)	USNM836526, MCZ238056	Marginal	–
Pinna rudis Linnaeus, 1758	MZSP114038	Marginal	–
Streptopinna saccata (Linnaeus, 1758)	USNM793744, USNM780031	Marginal	–
Plicatulidae Gray, 1857			
Plicatula gibbosa Lamarck, 1801	USNM801020, USNM801022	Marginal	Submarginal
Propeamussiidae Abbott, 1954			
Catillopecten eucymatus (Dall, 1898)	MCZ361432	–	Submarginal
Cyclopecten hoskynsi (Forbes, 1844)	ZUECBIV5702	–	Submarginal
Parvamussium cancellatum (E. A. Smith, 1885)	USNM803323, USNM856966	–	Submarginal

Table 1 (continued)

Taxa	Catalog number	IFT	MFT
Parvamussium pourtalesianum (Dall, 1886)	ZUECBIV2265, USNM856965	–	Submarginal
Propeamussium dalli (E. A. Smith, 1885)	USNM803326, USNM856943	–	Submarginal
Propeamussium lucidum (Jeffreys in Wyville-Thomson, 1873)	MCZ361413	–	Submarginal
Propeamussium meridionale (E. A. Smith, 1885)	USNM897961	–	Submarginal
Propeamussium sp.	USNM803320, USNM856941	–	Submarginal
Similipecten nanus (Verrill and Bush [in Verrill], 1897)	ZUECBIV2269, USNM803327	–	Submarginal
Pteriidae Gray, 1847 (1820)			
Pteria brevialata (Dunker, 1872)	MZSP55575, USNM836352	Marginal	Marginal
Pteria colymbus Röding, 1798	USNM801027	Marginal	Marginal
Pteria hirundo (Linnaeus, 1758)	MZSP10885, ZUECBIV1401	Marginal	Marginal
Pteria penguin (Röding, 1798)	USNM801027	Marginal	Marginal
Spondylidae Gray, 1826			
Spondylus americanus Hermann, 1781	USNM833744, USNM804280	Marginal	Submarginal
Spondylus senegalensis Schreibers, 1793	USNM1086035	Marginal	Submarginal
Spondylus squamosus Schreibers, 1793	USNM793728	Marginal	Submarginal
Vulsellidae Gray, 1854			
Electroma alacorvi (Dillwyn, 1817)	USNM700050, USNM801689	Marginal	Marginal
Electroma papilionacea (Lamarck, 1819)	USNM616482	Marginal	Marginal
Vulsella minor Röding, 1798	USNM896263	Marginal	Marginal
Vulsella vulsella (Linnaeus, 1758)	MZSP896263	Marginal	Marginal

IFT inner fold tentacles, *MCZ* Museum of Comparative Zoology, *MFT* middle fold tentacles, *MZSP* Museum of Zoology of the University of São Paulo, *SBMNH* Santa Barbara Museum of Natural History, *USNM* Smithsonian National Museum of Natural History, *ZUEC-BIV* Museum of Zoology "Prof. Adão José Cardoso" of the University of Campinas. Tentacle absence is indicated by "–". See Fig. 1 for schematic details of tentacle types

Adão José Cardoso" of the University of Campinas (ZUEC-BIV), Museum of Zoology of the University of São Paulo (MZSP), Smithsonian National Museum of Natural History (USNM), and Santa Barbara Museum of Natural History (SBMNH).

Nomenclature

In pteriomorphian bivalves, tentacles are repetitive organs located either on the inner mantle fold (Fig. 1b, c), on the middle mantle fold (Fig. 1d, e), or on both folds. Henceforward, they are named inner fold tentacles (IFT) and middle fold tentacles (MFT), depending on their location. In addition, tentacles originate either at the margin of the fold (marginal tentacles; Fig. 1b, d) or close to the margin (submarginal tentacles; Fig. 1c, e). Since tentacle origin and evolution should be discussed across different taxonomic levels, the names of orders, families, and superfamilies used throughout the following sections are indicated in Fig. 3 to facilitate data interpretation, in accordance with MolluscaBase (2020).

Character evolution

We used a previous phylogenetic study of Pteriomorphia with a broad taxonomic sampling (Audino et al. 2020b) to provide a phylogenetic framework to estimate tentacle evolution. A maximum likelihood tree for 197 pteriomorphian species (available in Dryad https://doi.org/10.5061/dryad.pk0p2ngjp) was used to perform ancestral state estimations in Mesquite Version 3.61 (Maddison and Maddison 2018). Tentacles were coded as present or absent according to their location in the mantle margin, i.e., on the inner mantle fold or on the middle mantle fold (Online Resource 1). Presence or absence of lateral branches, i.e., outgrowths from the main tentacular axis, were also considered (Online Resource 1). Not all taxa with molecular data could be analyzed morphologically due to unavailability of representative specimens in the analyzed museum collections. Thus, we designed our collection of morphological data to cover as many species and genera as possible from tentacled pteriomorphian families. Morphological states for 44 species with sequence data (ca. 22% of all taxa included in the phylogeny) were assigned based on the literature or as equivalent to congeneric species (taxa indicated in bold in Online Resource 1). In addition, body position relative to the substrate was coded based on information from literature about the orientation of the midsagittal plane, i.e., perpendicular to the substrate or at a low angle (parallel) to the substrate (Fig. 2c, d; Online Resource 1).

Ancestral state estimations were performed under maximum likelihood, adopting the symmetric model (Symm) that assumes equal rates for any particular change between states. This one-parameter model (Symm) presented a better fit to our data according to the likelihood ratio test (summarized in Online Resource 2) when compared to the asymmetrical two-parameter model (Asymm), which allows different transition rates (Pagel 1999; Maddison and Maddison 2018).

Likelihood scores (LS) were estimated for tentacle presence at ancestral nodes.

Results

Inner fold tentacles (IFT) occur in 11 out of 26 pteriomorphian families, while middle fold tentacles (MFT) are present in 15 families. Tentacle presence and location are summarized in Table 1. From a phylogenetic perspective, our results indicate that both IFT and MFT represent evolutionary convergences among pteriomorphian clades (Fig. 3). Moreover, they indicate that after being gained, tentacles have not been lost (Fig. 3).

Inner fold tentacles (IFT)

Distributed on the inner mantle fold (Fig. 1b, c), IFT were likely absent in the ancestor of Pteriomorphia and had four independent acquisitions in the ancestors of Ostreida (LS: 0.96), Plicatulidae (LS: 0.99), Spondylidae (LS: 098), and Pectinidae (LS: 0.99) (Fig. 3a). No evolutionary loss of IFT was estimated after their acquisition (Fig. 3a).

The Ostreida is the largest clade with numerous IFT. The order comprises the superfamilies Pinnoidea, Ostreoidea, and Pterioidea, all of them exhibiting numerous marginal IFT (Fig. 1b). In Pinnidae (pen shells), IFT are finger-like structures present only along the posterior portion of the mantle and vary in length and pigmentation across species (Fig. 4a, b). Oysters and relatives (Ostreoidea) have abundant IFT, which are long, numerous, and pigmented in the posteroventral zones, particularly close to the incurrent and excurrent regions (Fig. 4c–g). In Gryphaeidae (Fig. 4c, d), also known as honeycomb (foam) oysters, IFT are usually shorter than in Ostreidae (true oysters; Fig. 4e–g). The Pterioidea (pearl oysters and relatives) comprises Isognomonidae, Malleidae, Margaritidae, Pteriidae, and Vulsellidae. In all these families, tentacles are abundant and relatively longer in the posteroventral than the anterior region, exhibiting great variation in pigmentation among taxa (Fig. 4h–l). In *Pinctada* (Margaritidae) and *Pteria* (Pteriidae), ventral IFT have lateral branches and are slightly flattened (Fig. 4j–l), unlike the cone-shaped, unbranched tentacles of the other pterioidean

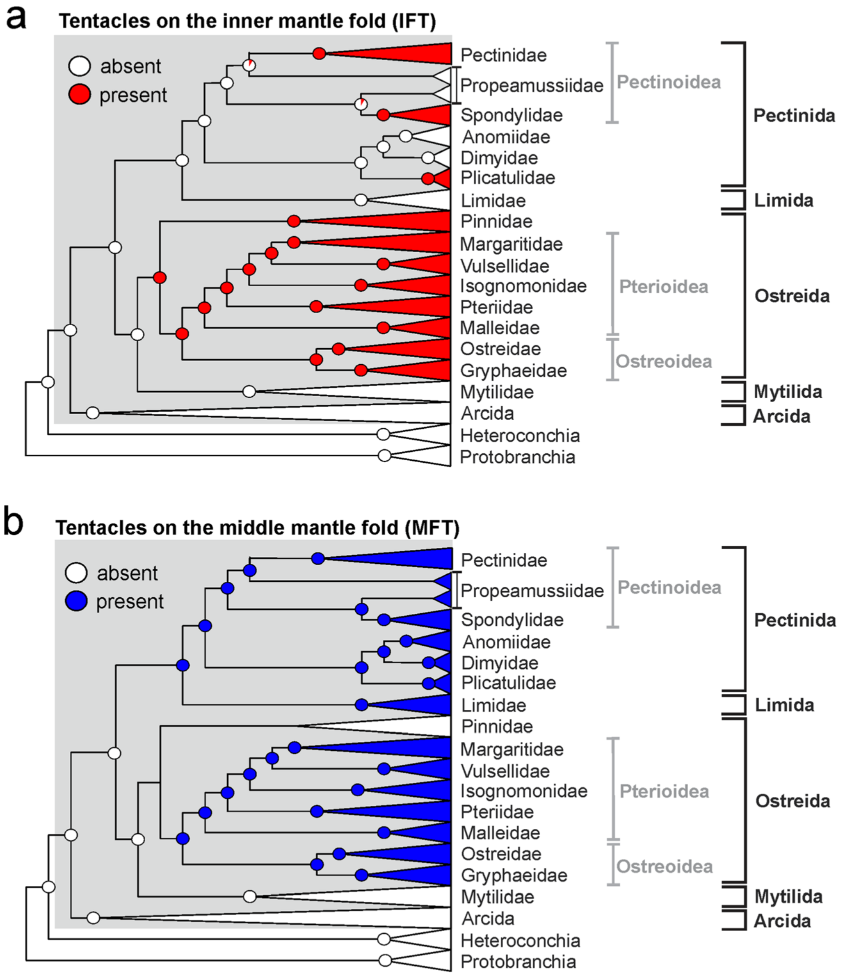

Fig. 3 Tentacle evolution in Pteriomorphia (Bivalvia). Maximum likelihood estimations of inner fold tentacles (IFT) in **a** and middle fold tentacles (MFT) in **b**. The clade Pteriomorphia is indicated by the gray box. Family names are in black, superfamily names in gray, and orders in bold. Likelihood proportions for ancestral states (presence and absence) are indicated in pie charts. **a** Four independent gains of IFT: in the ancestor of Pectinidae, in the ancestor of Spondylidae, in the ancestor of Plicatulidae, and in the ancestor of all Ostreida. **b** Two independent gains of MFT: in the ancestor of Pectinida + Limida and in the ancestor of the clade Ostreoidea + Pterioidea

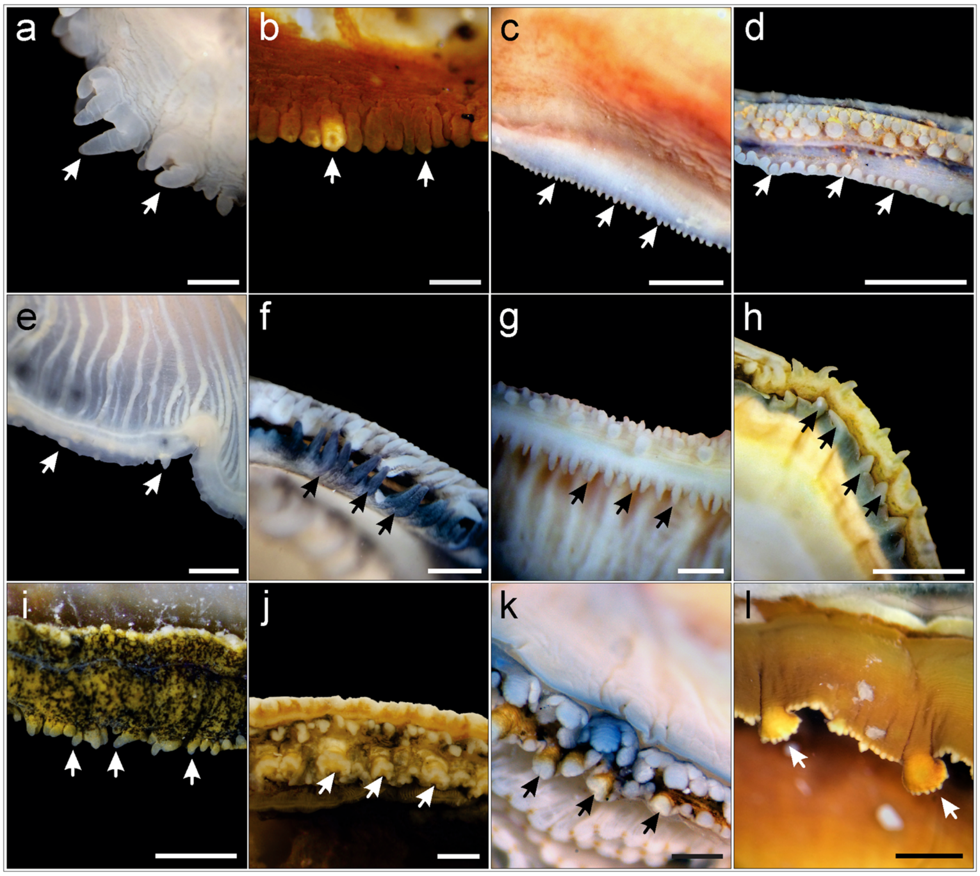

Fig. 4 Inner fold tentacles (IFT) in Ostreida (arrows). Marginal tentacles in Pinnidae (**a**–**b**), Gryphaeidae (**c**–**d**), Ostreida (**e**–**g**), Isognomonidae (**h**–**i**), Pteriidae (**j**), Margaritidae (**k**–**l**). Scale bars = 1 mm. **a** *Atrina rigida* (USNM847971). **b** *Pinna rudis* (MZSP114038). **c** *Neopycnodonte cochlear* (MCZ379076). **d** *Hyotissa mcgintyi* (USNM804282). **e** *Lopha cristagalli* (USNM793723). **f** *Striostrea prismatica* (SBMNH211884). **g** *Ostrea permollis* (USNM850800). **h** *Isognomon ephippium* (USNM701010). **i** *Isognomon isognomum* (MZSP54988). **j** *Pteria heteroptera* (MZSP55575). **k** *Pinctada imbricata* (ZUEC-BIV2383). **l** *Pinctada margaritifera* (USNM836493)

families (Fig. 4h, i). While IFT are of single-origin (according to our ancestral state estimation) and likely homologous across the Ostreida, lateral branches represent convergent gains in Margaritidae and Pteriidae (Online Resource 3).

In Pectinida, our ancestral state estimation indicates that IFT were independently gained in three lineages (Fig. 3a). In these clades, IFT show marked variation in size and position on the fold, i.e., marginal or submarginal. In *Plicatula gibbosa* Lamarck, 1801 (Plicatulidae), marginal IFT appear greatly reduced in size, likely an artifact due to the preservation method. They are also present in Spondylidae (thorny oysters), as marginal papillae uniformly distributed along the inner fold margin (Fig. 5a–c). Unlike other pteriomorphians, the Pectinidae (scallops) have submarginal IFT located on the outer surface of the inner fold (Fig. 1c). These tentacles vary greatly in shape, number, pigmentation, and position across species (Fig. 5d–o). For instance, in representatives of *Amusium*, *Crassodoma*, *Euvola*, *Palliolum*, *Pecten*, and *Pedum*, the IFT are organized in a single row of tentacles (Fig. 5d–g). In contrast, in the genera *Aequipecten*, *Argopecten*, *Chlamys*, *Gloripallium*, and *Placopecten*, IFT are usually organized in two rows, with proximal, short tentacles (Fig. 5h–k; arrows) and distal, long tentacles (Fig. 5h–k; arrowheads). A third, less common condition includes numerous small tentacles distributed over the fold's outer surface, as observed in *Adamussium colbecki* (E. A. Smith, 1902), *Delectopecten vitreus* (Gmelin, 1791), and *Zygochlamys patagonica* (P. P. King, 1832) (Fig. 5l–o).

Middle fold tentacles

Located on the middle mantle fold (Fig. 1d, e), MFT were likely absent in the ancestor of Pteriomorphia and had two distinct origins in the ancestor of the clades Ostreoidea + Pterioidea (LS: 0.98) and Pectinida + Limida (LS: 0.99) (Fig. 3b). No evolutionary loss of MFT was estimated after their acquisition (Fig. 3b).

In Ostreoidea (oysters and relatives), MFT are submarginal (Fig. 1e). They are frequently similar in shape and size to IFT, particularly in the ventral region, although MFT are usually less pigmented (Fig. 6a–f). Longer MFT (Fig. 6a–f; arrows) are proximally located, while shorter MFT (Fig. 6a–f; arrowheads) are distributed at a distal position, adjacent to the fold's margin, as observed in species of Ostreidae (Fig. 6a–d) and Gryphaeidae (Fig. 6e–f). Among Pterioidea (pearl oysters and relatives), MFT are marginal (Fig. 1d), uniform in size, and more densely distributed along the ventral region, as observed in Malleidae (Fig. 6g), Pteriidae (Fig. 6h), Isognomonidae (Fig. 6i), Margaritidae (Fig. 6j), and Vulsellidae (Fig. 6k–l).

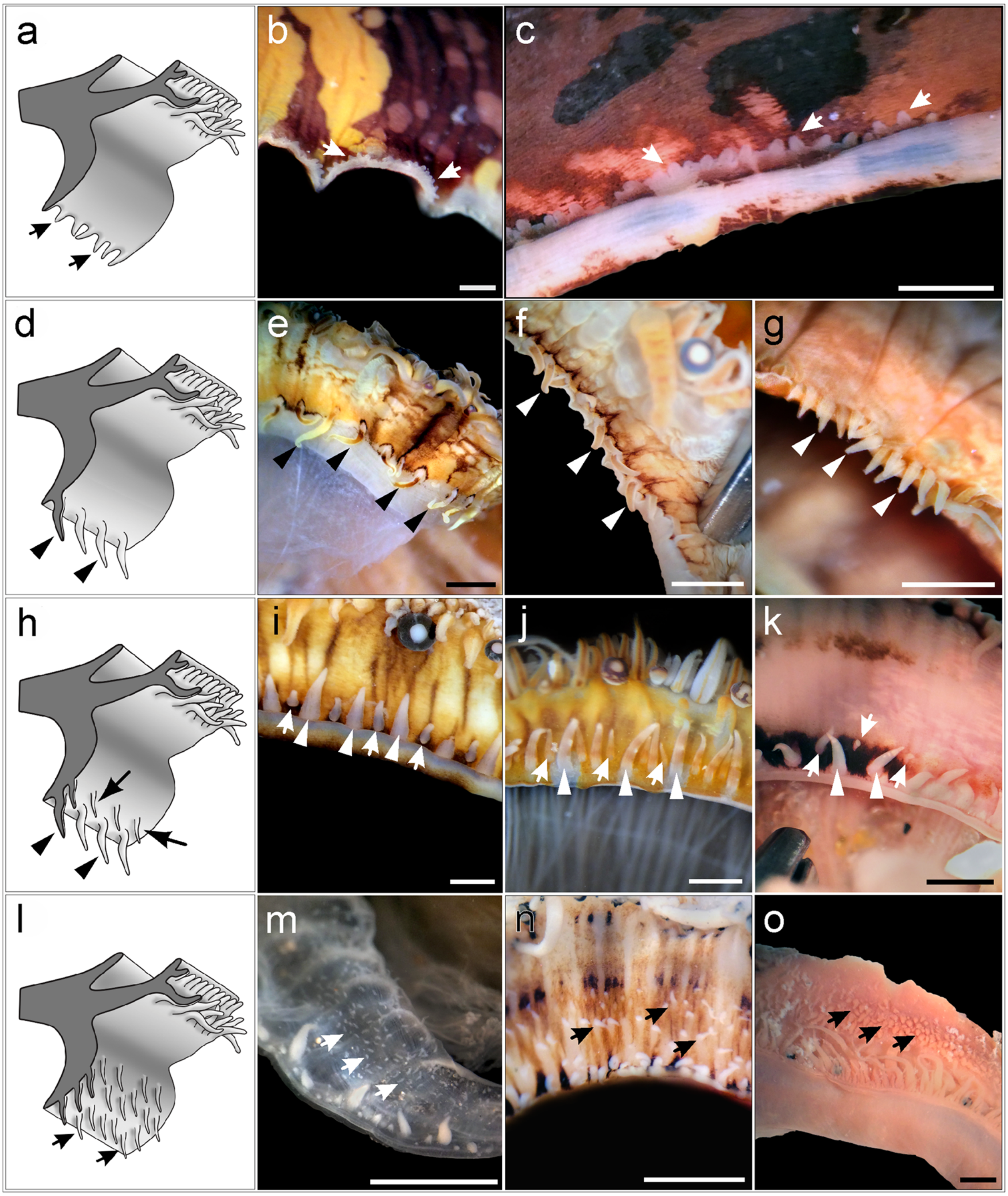

Fig. 5 Inner fold tentacles (IFT) in Pectinida. Marginal tentacles in Spondylidae (**a**–**c**) and submarginal in Pectinidae (**d**–**o**). Scale bars = 1 mm. **a** Schematic representation of marginal IFT (arrows), as observed in **b** and **c**. **b** *Spondylus americanus* (USNM833744). **c** *Spondylus squamosus* (USNM793728). **d** Schematic representation of submarginal IFT (arrowheads) in a single row, as observed in **e**–**g**. **e** *Euvola raveneli* (USNM801009). **f** *Amusium sp.* (USNM804083). **g** *Crassodoma gigantea* (SBMNH466682). **h** Schematic representation of submarginal IFT in two rows, with proximal (arrows) and distal (arrowheads) tentacles, as observed in **i**–**k**. **i** *Argopecten irradians* (MCZ278251). **j** *Aequipecten muscosus* (USNM855448). **k** *Gloripallium pallium* (USNM701201). **l** Schematic representation of submarginal IFT (arrows) over the outer surface, as observed in **m**–**o**. **m** *Delectopecten vitreus* (USNM757159). **n** *Zygochlamys patagonica* (USNM886527). **o** *Adamussium colbecki* (USNM886965)

The clade Limida, exclusively comprised by the family Limidae (file clams), exhibits submarginal MFT (Fig. 1e), which can be greatly enlarged, forming long organs densely distributed in up to five rows (Fig. 7a–e). Tentacles gradually enlarge from distal to proximal rows (Fig. 7a–e; arrowheads and arrows, respectively). Pigmentation varies from pale white and yellow (e.g., Fig. 7a) to orange and red (e.g., Fig. 7b). In some genera, such as *Acesta*, *Lima*, and *Ctenoides*,

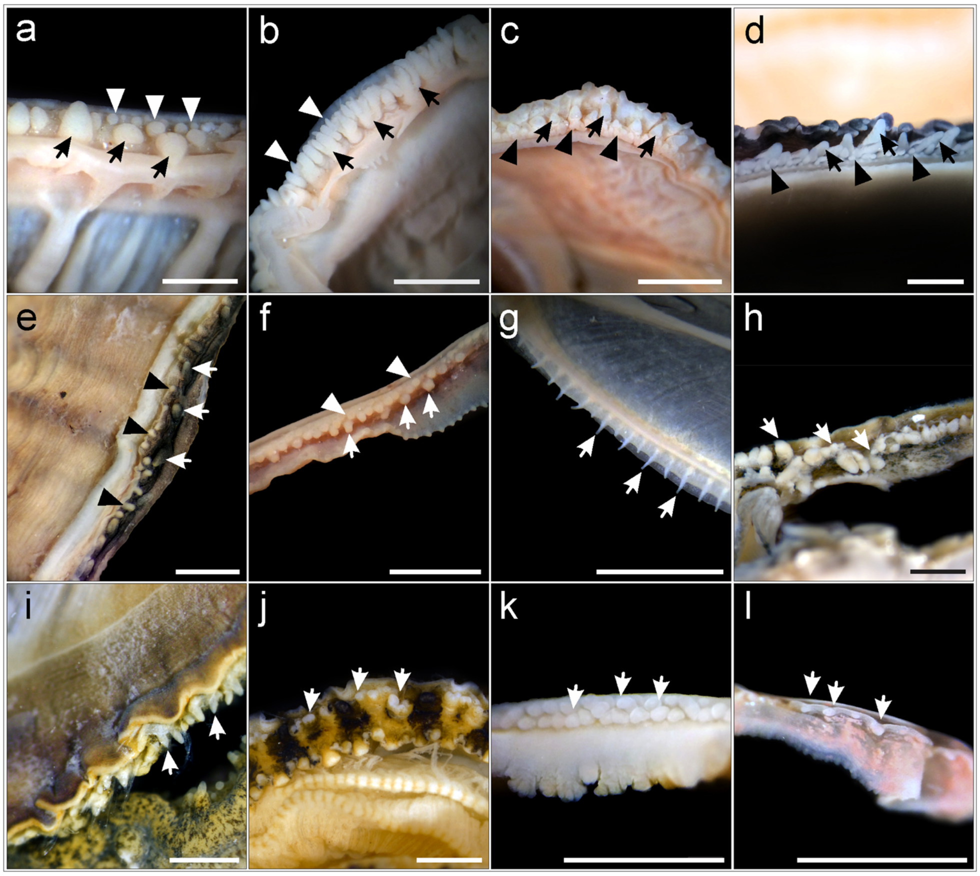

Fig. 6 Middle fold tentacles (MFT) in Ostreida. Submarginal tentacles in Ostreidae (**a**–**d**) and Gryphaeidae (**e**–**f**) and marginal tentacles in Malleidae (**g**), Pteriidae (**h**), Isognomonidae (**i**), Margaritidae (**j**), and Vulsellidae (**k**–**l**). Submarginal tentacles include proximal (arrows) and distal (arrowheads) tentacles (**a**–**f**). Marginal tentacles are indicated by arrows in **g**–**l**. Scale bars = 1 mm. **a** *Ostrea edulis* (USNM836256). **b** *Crassostrea virginica* (USNM804279). **c** *Dendostrea folium* (USNM802346). **d** *Striostrea prismatica* (SBMNH211884). **e** *Hyotissa hyotis* (MCZ378999). **f** *Neopycnodonte cochlear* (MCZ379076). **g** *Malleus candeanus* (MCZ340681). **h** *Pteria hirundo* (ZUEC-BIV1401). **i** *Isognomon isognomum* (MZSP54988). **j** *Pinctada imbricata* (MZSP106549). **k** *Vulsella minor* (USNM896263). **l** *Electroma alacorvi* (USNM801689)

tentacles are papillose, with protuberances on the surface (e.g., Fig. 7d). A longitudinal groove (Fig. 7; indicated by the symbol “>”) was observed along the tentacles of *Acesta* (Fig. 7c), *Ctenoides* (Fig. 7d), *Limaria* (Fig. 7e), and *Limatula* (Fig. 7a). An annulated pattern is also present in the MFT of *Limatula* (Fig. 7a) and *Limaria* (Fig. 7e).

The Pectinida encompasses Anomiidae, Dimyidae, Plicatulidae, Pectinidae, Propeamussiidae, and Spondylidae. In these groups, MFT are submarginal, occupying proximal to distal positions on the inner surface of the middle fold (Fig. 1e). In *Dimya argentea* Dall, 1886 (Dimyidae), MFT are small and sparsely distributed in a single row (Fig. 7f). In *Plicatula gibbosa* (Plicatulidae), tentacles are more abundant, including short (distal) and long (proximal) tentacles in two rows (Fig. 7g; arrowheads and arrows, respectively). In the Anomiidae, MFT are abundant and distributed along three rows, the proximal ones showing larger tentacles (Fig. 7h–j; arrows). In scallops and relatives (i.e., Pectinidae, Propeamussiidae, and Spondylidae), MFT are organized in multiple rows, being abundant and shorter distally (Fig. 7k–p; arrowheads) and much longer proximally (Fig. 7k–p, arrows). Numerous mirror eyes are also proximally located on the middle fold (Fig. 7k, m–p), their eyestalks likely representing modified proximal tentacles. Despite great variation in MFT pigmentation and abundance, MFT position over the fold, with multiple rows, is conserved across pectinid species, in contrast to their more morphologically diverse IFT.

Body position relative to the substrate

Ancestral state estimation suggests that the ancestor of Pteriomorphia was likely positioned with the midsagittal plane perpendicular to the substrate (Fig. 8a). This position is observed in several bivalves, such as mussels (Mytilidae) and ark clams (Arcidae), in which the byssal attachment pulls the ventral body region towards the substrate (Fig. 8b). Consequently, the anteroventral mantle margin faces the substrate along with the shell edge. Independent changes in body position were estimated for the ancestors of the clades Pectinida + Limida and Ostreoidea + Pterioidea (Fig. 8a). In this case, the byssal attachment is anterior and the midsagittal plane is oriented at a low angle to the substrate, nearly parallel, with one valve supporting the body (Fig. 8c). Therefore, most of the mantle margin is exposed to the surrounding environment. These two shifts of body position relative to the substrate coincide with independent acquisitions of MFT within Pteriomorphia (Fig. 8d).

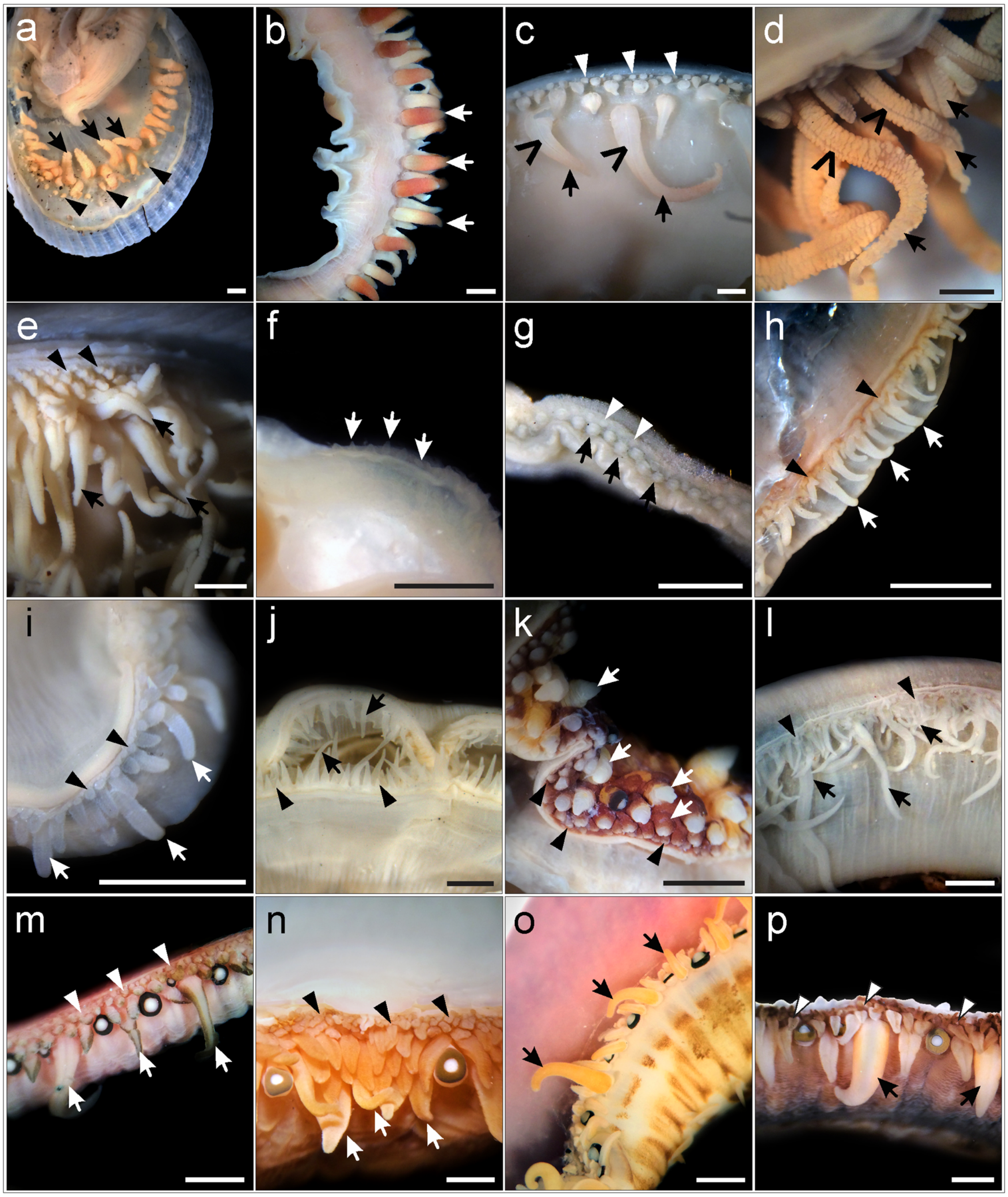

Fig. 7 Middle fold tentacles (MFT) in Pectinida. Proximal (arrows) and distal (arrowheads) submarginal tentacles in Limidae (**a**–**e**), Dimyidae (**f**), Plicatulidae (**g**), Anomiidae (**h**–**j**), Spondylidae (**k**), Propeamussiidae (**l**), and Pectinidae (**m**–**p**). Longitudinal grooves are indicated by ">". Scale bars = 1 mm. **a** *Limatula hodgsoni* (USNM882395). **b** *Lima lima* USNM754383. **c** *Acesta oophaga* (USNM1263635). **d** *Ctenoides scaber* (USNM833716). **e** *Limaria orbignyi* (SBMNH19892). **f** *Dimya argentea* (USNM855224). **g** *Plicatula gibbosa* (USNM801022). **h** *Pododesmus macrochisma* (SBMNH361457). **i** *Pododesmus rudis* (USNM850821). **j** *Anomia simplex* (ZUEC-BIV1423). **k** *Spondylus senegalensis* (USNM1086035). **l** *Propeamussium dalli* (USNM856943). **m** *Placopecten magellanicus* (USNM829091). **n** *Crassodoma gigantea* (SBMNH466682). **o** *Palliolum tigerinum* (MCZ376695). **p** *Chlamys hastata* (USNM739716)

Discussion

Based on a broad sampling of tentacle morphology in pteriomorphians, our study represents the first attempt to investigate bivalve tentacles in a broad phylogenetic-based context. In addition, our morphological survey expands the knowledge of soft anatomy for less studied bivalve taxa, particularly Anomiidae, Dimyidae, Gryphaeidae, Limidae, Malleidae, Plicatulidae, and Propeamussiidae.

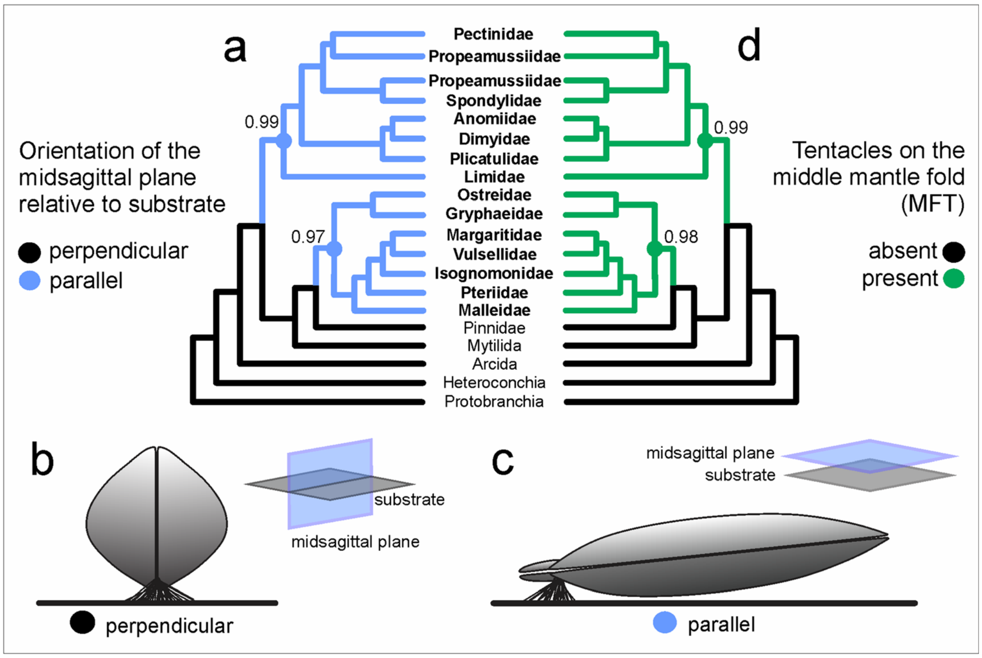

Fig. 8 Evolution of body position and tentacles in Pteriomorphia (Bivalvia). The midsagittal plane defines the left and right sides of the bivalve body. Taxa names in bold indicate presence of middle fold tentacles (MFT) and midsagittal plane parallel to the substrate. Numbers above selected nodes indicate the likelihood score of the corresponding state. **a** Estimation of changes in the midsagittal plane orientation relative to the substrate (body position). The ancestor of Pteriomorphia likely had the midsagittal plane perpendicular to the substrate, making the ventral mantle region, along with the shell's edge, face the surface. This is the typical position adopted by many epifaunal bivalves, such as mussels and ark clams (**b**). In two independent events, the midsagittal plane orientation was shifted to nearly parallel. In scallops, file clams, oysters, and relatives, the body is supported by one valve only, leaving most mantle margin exposed (**c**). **d** Same reconstruction indicated in Fig. 3b for MFT

Tentacle evolution and associated functions

Our results suggest that mantle tentacles are not homologous in Pteriomorphia because IFT have evolved at least four times independently, while MFT likely had two distinct origins. Even though mantle tentacles exhibit a complex organization, we have scored them as present or absent to facilitate a holistic approach, providing a first step to discuss tentacle evolution in bivalves. Although our results argue against tentacle homology in pteriomorphians due to different phylogenetic origins, it is relevant to note that apparent independent acquisitions (homoplasies) may be explained by shared genetic regulatory systems (Shubin et al. 2009). Consequently, further investigations should test for common origin at other biological levels to fully corroborate or refute a homology hypothesis (Ochoterena et al. 2019). In the case of bivalve tentacles, detailed investigations focused on tentacle development are necessary to elucidate their mechanisms of formation and possible common developmental pathways. In addition, future studies considering gene and protein expression should shed light on the specificity of tentacle tissues and receptors, contributing to identify common functions and sensory receptor diversity.

Along with other mantle traits, such as eyes (Audino et al. 2020b) and siphons (Yonge 1983), tentacles illustrate the diversity of the bivalve mantle and its complicated evolution. These findings add to the increasing body of evidence showing evolutionary convergences as common phenotypic outcomes among bivalves, as demonstrated for lifestyles (Morton 1990; Alejandrino et al. 2011; Audino et al. 2019), shell shape (Stanley 1970; Owada 2007; Serb et al. 2017), chemosymbiosis (Taylor and Glover 2010), and photosymbiosis (Li et al. 2020). Interestingly, once lineages gain tentacles, they do not lose them, which suggests that tentacles and their associated functions have adaptive significance during the evolution of pteriomorphians.

The origin and maintenance of IFT might be associated, for example, with protection of the mantle cavity, as well as with sensory perception (Yonge 1983; Sartori and Domaneschi 2005). When the valves are opened and the mantle aperture is exposed, IFT from right and left lobes remain interlocked, creating a physical barrier that prevents the entrance of large particles into the mantle cavity (Yonge 1968). In bivalves living buried in the substrate, an analogous condition is observed with simple and branched tentacles that help to protect the incurrent aperture from larger particles (Fishelson 2000; Sartori and Domaneschi 2005; Sartori et al. 2008; Vitonis et al. 2012). IFT also have numerous nerves associated with ciliary tufts on the tentacle surface. These structures are likely sensory receptors, suggesting that IFT in oysters and relatives have sensory functions (Audino and Marian 2020).

Similarly, several lines of evidence suggest that MFT have sensory roles, as expected for organs located on the middle mantle fold (Yonge 1983). For example, MFT in Ostreoidea and Pterioidea are organs provided with multiple tentacular nerves and sensory receptors, particularly at the tip of the tentacle where a group of ciliary receptors is located (Audino and Marian 2020). In scallops (Pectinidae), long MFT were observed in *Argopecten irradians* (Lamarck, 1819) (Wilkens 2006), *Nodipecten nodosus* (Linnaeus, 1758) (Audino et al. 2015), *Pecten maximus* (Linnaeus, 1758) (Dakin 1909), and *Placopecten magellanicus* (Gmelin, 1791) (Moir 1977). Roles of mechano- and chemoreception have been attributed to the MFT of these species based on different lines of evidence. For example, anatomical investigation revealed innervation of ciliary receptors in the MFT of scallops, particularly in the ciliated papillae located on the distal third of the tentacle (Moir 1977; Audino et al. 2015). Additionally, behavioral assays showed that the contact of MFT of scallops with living predators and starfish extracts is able to trigger escape responses, suggesting mechano- and chemoreception roles (Gutsell 1931; Thomas and Gruffydd 1971; Wilkens 2006). In the case of file clams (Limidae), the very enlarged MFT in *Limaria* species are not only sensorial but have been attributed further functions, such as to support the body, facilitate swimming movements, and act as defensive structures against predators by autotomy and secretion of noxious substances (Gilmour 1967; Morton 1979; Owen and McCrae 1979; Donovan et al. 2004).

Comparative morphology of tentacles

In oysters and relatives (Ostreoidea), comparative studies among *Crassostrea* species revealed uniform morphology of marginal IFT, with a tendency to increase size towards the ventral region (Amaral and Simone 2014). We also observed this pattern in all examined genera of Ostreidae and Gryphaeidae. In both families, MFT are submarginal and distributed along two rows, as previously noted for *Hyotissa mcgintyi* (Harry, 1985) (Gryphaeidae) and oyster species of *Crassostrea*, *Ostrea*, and *Saccostrea* (Dinamani 1971; Tëmkin 2006; Amaral and Simone 2014; Simone et al. 2015; Audino and Marian 2020).

Our results for Pterioidea, combined with previous data (Yonge 1968; Morton 1995; Tëmkin 2006), expand the current knowledge of tentacles for the clade. In a phylogenetic investigation, mantle tentacles have been recovered as a shared trait between Ostreoidea and Pterioidea (Tëmkin 2006). Anatomical details, such as branching tentacular nerves and ciliary receptors at the tentacle tips, also suggest that mantle tentacles are homologous in those clades (Audino and Marian 2020), consistent with our ancestral state estimations (Fig. 3). Lateral branches on IFT seem to be restricted to *Pinctada* (Margaritidae) and *Pteria* (Pteriidae), as observed by others (Morton 1995; Tëmkin 2006; Audino and Marian 2020). Our results complement these observations, suggesting convergent gains of lateral branches in Margaritidae and Pteriidae (Online Resource 3).

In contrast to oyster and relatives, all Pinnidae (pen shells) have marginal IFT restricted to the posterior region, the middle fold being devoid of tentacles (Grave 1911; Yonge 1953; Audino and Marian 2020; present study). Interestingly, pinnids are semi-infaunal bivalves that bury the anterior body region into the substrate, leaving only the posterior region exposed, where the incurrent and excurrent apertures are located (Yonge 1953).

In the Pectinida, IFT were not observed in any examined species of Anomiidae, Dimyidae, and Propeamussiidae. Attention to the absence of IFT has been previously drawn for some propeamussiids (Waller 1978; Morton and Thurston 1989). Very small papillae, greatly reduced due to preservation, are present in Plicatulidae, as previously observed in *Plicatula gibbosa* (Yonge 1973) and *Plicatula australis* Lamarck, 1819 (Simone and Amaral 2008). Similarly, the Spondylidae (thorny oysters) exhibit IFT as numerous, small papillae along the entire margin. The anatomy of these structures was previously described for *Spondylus ictericus*, including muscular organization and cilia distribution (Audino and Marian 2020). In Pectinidae (scallops), IFT were reported for *Argopecten irradians* (Gutsell 1931), *Nodipecten nodosus* (Audino et al., 2015), and *Placopecten magellanicus* (Moir 1977) as a row of tentacles occurring close to the mantle margin. However, our survey has demonstrated a surprising diversity of IFT among scallops (Fig. 5d, h, l). Interestingly, these different spatial patterns of IFT do not seem to be tied to lifestyles (Alejandrino et al. 2011), and particularly the small tentacles distributed over the fold's surface (Fig. 5l) might represent convergent gains since the corresponding species are not closely related to each other in the Pectinidae (Sherratt et al. 2016). These findings should stimulate further studies to clarify the evolution of this tentacular diversity.

All taxa from the orders Pectinida and Limida have submarginal MFT distributed along the entire mantle margin. In Limidae, multiple rows of MFT have been described for species of *Lima* and *Ctenoides* (Morton 1979; Mikkelsen and Bieler 2003), the latter with longitudinal grooves, which we also observed in *Acesta*, *Limaria*, and *Limatula*. Annulated tentacles have been previously reported in *Limaria* species (Gilmour 1963; Waller 1976; Morton 1979), and we also observed their presence in *Limatula*. The diversity of tentacle morphology in limids still requires further investigation with a comprehensive taxonomic sampling to understand the evolution and variation of these unique traits.

In Plicatulidae and Dimyidae, MFT were previously described as small papillae (Yonge 1973, 1975; Simone and Amaral 2008), occurring in two rows, which is consistent with our observations for additional species. In the Anomiidae, tentacle information was previously restricted to species of *Pododesmus* (Holmes 2017). Our observations indicate long and abundant tentacles forming three rows in this genus, and comparatively longer organs in *Anomia simplex* d'Orbigny, 1853 and *Heteranomia squamula* (Linnaeus, 1758).

Middle fold tentacles and body position on the substrate

The position of the body relative to the substrate is regarded as a key feature in the diversification of bivalve body shapes and lifestyles (Yonge 1962; Stanley 1970, 1972; Seilacher 1984). In pteriomorphians, two positions are related to physical stabilization on the substrate, i.e., midsagittal plane of the body perpendicular or at low angle (parallel) to the substrate (Fig. 8b, c) (Stanley 1972). Fossil evidence for different extinct groups related to the living pteriomorphian families suggests the transition from perpendicular orientation of the midsagittal plane to forms that came to rest upon one valve (Stanley 1972), which is in accordance with our ancestral state estimation (Fig. 8a). This transition is associated with major morphological changes, such as anterior byssal attachment, rounded shells, and reduced (or event absent) anterior adductor musculature (Stanley 1972; Seilacher 1984; Oliver and Holmes 2006; Owada 2007).

Our analyses show that independent transitions from perpendicular to parallel position coincide with convergent acquisitions of MFT, but not IFT, in the ancestors of two pteriomorphian clades (Fig. 8). We are aware that the observed pattern of co-distribution should be interpreted cautiously, because it does not provide definite evidence for dependent evolution between traits (Maddison and FitzJohn 2015). Even though our initial hypothesis has not been refuted, further investigations are necessary to elucidate possible associations between these conditions. So far, our results suggest a plausible evolutionary scenario where the parallel position on the substrate, with the body reclined upon one valve, could have resulted in exposure of almost the entire mantle margin to the surrounding environment, therefore providing more area to the development of repeated sensory organs (Kauffman 1969).

Conclusions

Our data indicate that MFT and IFT are convergent acquisitions in separate pteriomorphian clades, representing repeated evolution of mantle organs across different taxonomic levels. These results reinforce the plasticity of the molluscan body (Wanninger et al. 2008) and the relevance of evolutionary convergences in the radiation of bivalve groups (Stanley 1970; Distel 2000; Oliver and Holmes 2006; Owada 2007; Alejandrino et al. 2011; Serb et al. 2017; Audino et al. 2019, 2020a; Smith et al. 2020). We also found that MFT evolution coincides with shifts to parallel orientation of the midsagittal plane on the substrate, an innovation during diversification of epifaunal bivalves.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13127-021-00482-3.

Acknowledgments The authors acknowledge the grants 2015/09519-4 and 2017/01365-3, São Paulo Research Foundation (FAPESP) (to JAA and JEARM), and the National Science Foundation (DEB 1754331) (to JMS). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 (to JAA and JEARM). This study is part of the first author's Doctorate's thesis through the Graduate Program in Zoology of the Institute of Biosciences (University of São Paulo). The authors thank the following institutions that provided materials for the development of this study: Museum of Comparative Zoology (MCZ), Museum of Zoology "Prof. Adão José Cardoso" of the University of Campinas (ZUEC), Museum of Zoology of the University of São Paulo (MZSP), Santa Barbara Museum of Natural History (SBMNH), and Smithsonian National Museum of Natural History (USNM). The authors also acknowledge the helpful comments and suggestions provided by Dr. Reuben Shipway and an anonymous reviewer. This is a contribution of NP-BioMar (Research Center for Marine Biodiversity – USP).

Code availability Not applicable.

Authors' contributions All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Jorge A. Audino. The first draft of the manuscript was written by Jorge A. Audino, and all authors commented on and edited previous versions of the manuscript. All authors read and approved the final manuscript.

Funding São Paulo Research Foundation (FAPESP), grant 2015/09519-4 and 2017/01365-3. Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. National Science Foundation (NSF), grant DEB 1754331.

Data availability All data generated or analyzed during this study are included in this article (Table 1) and its supplementary information (Online Resources 1–3). Phylogenetic tree used in the study is publicly archived in Dryad under the DOI https://doi.org/10.5061/dryad.pk0p2ngjp.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Agrawal, A. A. (2017). Toward a predictive framework for convergent evolution: Integrating natural history, genetic mechanisms, and consequences for the diversity of life. *The American Naturalist, 190*, S1–S12.

Alejandrino, A., Puslednik, L., & Serb, J. M. (2011). Convergent and parallel evolution in life habit of the scallops (Bivalvia: Pectinidae). *BMC Evolutionary Biology, 11*, 164.

Amaral, V. S. D., & Simone, L. R. L. (2014). Revision of genus *Crassostrea* (Bivalvia: Ostreidae) of Brazil. *Journal of the Marine Biological Association of the United Kingdom, 94*, 811–836.

Audino, J. A., & Marian, J. E. A. R. (2018). Comparative and functional anatomy of the mantle margin in ark clams and their relatives (Bivalvia: Arcoidea) supports association between morphology and life habits. *Journal of Zoology, 305*, 149–162.

Audino, J. A., & Marian, J. E. A. R. (2020). Form and function of tentacles in pteriomorphian bivalves. *Journal of Morphology, 281*, 33–46.

Audino, J. A., Serb, J. M., & Marian, J. E. A. R. (2019). Ark clams and relatives (Bivalvia: Arcida) show convergent morphological evolution associated with lifestyle transitions in the marine benthos. *Biological Journal of the Linnean Society, 126*(4), 866–884.

Audino, J. A., Serb, J. M., & Marian, J. E. A. R. (2020a). Phylogeny and anatomy of marine mussels (Bivalvia: Mytilidae) reveal convergent evolution of siphon traits. *Zoological Journal of the Linnean Society, 190*(2), 592–612.

Audino, J. A., Serb, J. M., & Marian, J. E. A. R. (2020b). Hard to get, easy to lose: Evolution of mantle photoreceptor organs in bivalves (Pteriomorphia). *Evolution, 74*(9), 2105–2120.

Audino, J. A., Marian, J. E. A. R., Wanninger, A., & Lopes, S. G. B. C. (2015). Anatomy of the pallial tentacular organs of the scallop *Nodipecten nodosus* (Linnaeus, 1758) (Bivalvia: Pectinidae). *Zoologischer Anzeiger - A Journal of Comparative Zoology, 258*, 39–46.

Bieler, R., Carter, J. G., & Coan, E. V. (2010). Classification of bivalve families. *Malacologia, 52*, 113–133.

Bickell-Page, L. R., & Mackie, G. O. (1991). Tentacle autotomy in the hydromedusa *Aglantha digitale* (Cnidaria): An ultrastructural and neurophysiological analysis. *Philosophical Transactions of the Royal Society of London B, 331*, 155–170.

Carter, J. G., Harries, P. J., Malchus, N., Sartori, A. F., Anderson, L. C., Bieler, R., et al. (2012). Illustrated glossary of the Bivalvia. *Treatise Online, 48*, 1–209.

Schluter, D. (2000). The ecology of adaptive radiation. OUP Oxford.

Dakin, W. J. (1909). Pecten. Proceedings of the Liverpool Biological Society, 23, 332–468.

Dinamani, P. (1971). Occurrence of the Japanese oyster, *Crassostrea Gigas* (Thunberg), in northland, New Zealand. *New Zealand Journal of Marine and Freshwater Research, 5*, 352–357.

Distel, D. L. (2000). Phylogenetic relationships among Mytilidae (Bivalvia): 18S rRNA data suggest convergence in mytilid body plans. *Molecular Phylogenetics and Evolution, 15*, 25–33.

Donovan, D. A., Elias, J. P., & Baldwin, J. (2004). Swimming behavior and morphometry of the file shell *Limaria fragilis*. *Marine and Freshwater Behaviour and Physiology, 37*, 7–16.

Dougherty, L. F., Niebergall, A. K., Broeckling, C. D., Schauer, K. L., & Li, J. (2019). Brightly coloured tissues in limid bivalves chemically deter predators. *Royal Society Open Science, 6*(10), 191298.

Dubois, S., Barillé, L., Cognie, B., & Beninger, P. (2005). Particle capture and processing mechanisms in *Sabellaria alveolata* (Polychaeta: Sabellariidae). *Marine Ecology Progress Series, 301*, 159–171.

Fishelson, L. (2000). Comparative morphology and cytology of siphons and siphonal sensory organs in selected bivalve molluscs. *Marine Biology, 137*, 497–509.

Gilmour, T. H. J. (1963). A note on the tentacles of *Lima hians* (Gmelin) (Bivalvia). *Journal of Molluscan Studies, 35*, 82–85.

Gilmour, T. H. J. (1967). The defensive adaptations of *Lima hians* (Mollusca, Bivalvia). *Journal of the Marine Biological Association of the United Kingdom, 47*, 209–221.

Grave, B. H. (1911). Anatomy and physiology of the wing-shell, *Atrina rigida*. Bulletin of the Bureau of Fisheries (United States Bureau of Fisheries), 29, 409–439.

Gutsell, J. S. (1931). Natural history of the bay scallop. Bulletin of the Bureau of Fisheries (United States Bureau of Fisheries), 46, 569–632.

Harper, E. M., & Skelton, P. W. (1993). The Mesozoic marine revolution and epifaunal bivalves. *Scripta Geologica, 2*, 127–153.

Haszprunar, G., Kunze, T., Warén, A., & Heß, M. (2017). A reconsideration of epipodial and cephalic appendages in basal gastropods: Homologies, modules and evolutionary scenarios. *Journal of Molluscan Studies, 83*(4), 363–383.

Hodgson, A. N., & Fielden, L. J. (1984). The structure and distribution of peripheral ciliated receptors in the bivalve molluscs *Donax serra* and *D. sordidus*. *Journal of Molluscan Studies, 50*, 104–112.

Holmes, A. M. (2017). Phylogenetics of British saddle oysters (Bivalvia: Anomiidae) – A review of the shell morphology, internal anatomy and genetics of *Pododesmus* in British waters. *Journal of Conchology, 42*, 317–325.

Kauffman, E. G. (1969). Form, function, and evolution. In R. C. Moore (Ed.), *Treatise on invertebrate paleontology*, Part N, Mollusca 6 (pp. 120–205). Geol. Soc. Amer. and Univ. Kansas Press.

Kier, W. M. (2016). The musculature of coleoid cephalopod arms and tentacles. *Frontiers in Cell and Developmental Biology, 4*, 10.

Künz, E., & Haszprunar, G. (2001). Comparative ultrastructure of gastropod cephalic tentacles: Patellogastropoda, Neritaemorphi and Vetigastropoda. *Zoologischer Anzeiger – A Journal of Comparative Zoology, 240*, 137–165.

Kuzmina, T. V., & Temereva, E. N. (2019). Organization of the lophophore in the deep-sea brachiopod *Pelagodiscus atlanticus* and evolution of the lophophore in the Brachiozoa. *Organisms, Diversity and Evolution, 19*, 31–39.

Li, J., Lemer, S., Kirkendale, L., Bieler, R., Cavanaug, C., & Giribet, G. (2020). Shedding light: A phylotranscriptomic perspective illuminates the origin of photosymbiosis in marine bivalves. *BMC Evolutionary Biology, 20*, 50.

Machado, F. M., Morton, B., & Passos, F. D. (2017). Functional morphology of *Cardiomya cleryana* (d'Orbigny, 1842)(Bivalvia: Anomalodesmata: Cuspidariidae) from Brazilian waters: New insights into the lifestyle of carnivorous bivalves. *Journal of the Marine Biological Association of the United Kingdom, 97*(2), 447–462.

Maddison, W. P., & FitzJohn, R. G. (2015). The unsolved challenge to phylogenetic correlation tests for categorical characters. *Systematic Biology, 64*, 127–136.

Maddison, W. P., & Maddison, D. R. (2018). Mesquite: a modular system for evolutionary analysis. Version 3.51. http://www.mesquiteproject.org.

Mahler, D. L., Weber, M. G., Wagner, C. E., & Ingram, T. (2017). Pattern and process in the comparative study of convergent evolution. *The American Naturalist, 190*, S13–S28.

Mikkelsen, P. M., & Bieler, R. (2003). Systematic revision of the western Atlantic file clams, *Lima* and *Ctenoides* (Bivalvia: Limoida: Limidae). *Invertebrate Systematics, 17*, 667–710.

Moir, A. J. G. (1977). Ultrastructural studies on the ciliated receptors of the long tentacles of the giant scallop, *Placopecten magellanicus* (Gmelin). *Cell and Tissue Research, 184*, 367–380.

MolluscaBase eds. (2020). MolluscaBase. Accessed at http://www.molluscabase.org on 2020-07-15.

Morton, B. (1979). A comparison of lip structure and function correlated with other aspects of the functional morphology of *Lima lima*, *Limaria* (*Platilimaria*) *fragilis*, and *Limaria* (*Platilimaria*) *hongkongensis* sp.nov. (Bivalvia: Limacea). *Canadian Journal of Zoology, 57*, 728–742.

Morton, B. (1990). Corals and their bivalve borers—The evolution of a symbiosis. In B. Morton (Ed.), The Bivalvia—Proceedings of a memorial symposium in honour of Sir Charles Maurice Yonge, Edinburgh, 1986 (pp. 11–46). Hong Kong: Hong Kong University Press.

Morton, B. (1995). The biology and functional morphology of *Pteria brevialata* (Bivalvia: Pterioidea), epizoic on gorgonians in Hong Kong. *Journal of Zoology, 236*, 223–241.

Morton, B., & Peharda, M. (2008). The biology and functional morphology of *Arca noae* (Bivalvia: Arcidae) from the Adriatic Sea, Croatia, with a discussion on the evolution of the bivalve mantle margin. *Acta Zoologica, 89*, 19–28.

Morton, B., & Thurston, M. H. (1989). The functional morphology of *Propeamussium lucidum* (Bivalvia: Pectinacea), a deep-sea predatory scallop. *Journal of Zoology, 218*, 471–496.

Ochoterena, H., Vrijdaghs, A., Smets, E., & Claßen-Bockhoff, R. (2019). The search for common origin: Homology revisited. *Systematic Biology, 68*(5), 767–780.

Oliver, P. G., & Holmes, A. M. (2006). The Arcoidea (Mollusca: Bivalvia): A review of the current phenetic-based systematics. *Zoological Journal of the Linnean Society, 148*, 237–251.

Owada, M. (2007). Functional morphology and phylogeny of the rock-boring bivalves *Leiosolenus* and *Lithophaga* (Bivalvia: Mytilidae): A third functional clade. *Marine Biology, 150*(5), 853–860.

Owen, G., & McCrae, J. M. (1979). Sensory cell/gland cell complexes associated with the pallial tentacles of the bivalve *Lima hians* (Gmelin), with a note on specialized cilia on the pallial curtains. *Philosophical Transactions of the Royal Society B, 287*, 45–62.

Pagel, M. (1999). The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic Biology, 48*(3), 612–622.

Pellmyr, O., & Krenn, H. W. (2002). Origin of a complex key innovation in an obligate insect–plant mutualism. *Proceedings of the National Academy of Sciences, 99*(8), 5498–5502.

Roberts, D., & Moore, H. M. (1997). Tentacular diversity in deep-sea deposit-feeding holothurians: Implications for biodiversity in the deep sea. *Biodiversity and Conservation, 6*(11), 1487–1505.

Ruth, P., Schmidtberg, H., Westermann, B., & Schipp, R. (2002). The sensory epithelium of the tentacles and the rhinophore of *Nautilus pompilius* L.(Cephalopoda, Nautiloidea). *Journal of Morphology, 251*(3), 239–255.

Sartori, A. F., & Domaneschi, O. (2005). The functional morphology of the antarctic bivalve *Thracia meridionalis* Smith, 1885 (Anomalodesmata: Thraciidae). *Journal of Molluscan Studies, 71*, 199–210.

Sartori, A. F., Printrakoon, C., Mikkelsen, P. M., & Bieler, R. (2008). Siphonal structure in the Veneridae (Bivalvia: Heterodonta) with an assessment of its phylogenetic application and a review of venerids of the Gulf of Thailand. *The Raffles Bulletin of Zoology, 18*, 103–125.

Seilacher, A. (1984). Constructional morphology of bivalves: Evolutionary pathways in primary versus secondary soft-bottom dwellers. *Palaeontology, 27*, 207–237.

Serb, J. M., Sherratt, E., Alejandrino, A., & Adams, D. C. (2017). Phylogenetic convergence and multiple shell shape optima for gliding scallops (Bivalvia: Pectinidae). *Journal of Evolutionary Biology, 30*, 1736–1747.

Sherratt, E., Alejandrino, A., Kraemer, A. C., Serb, J. M., & Adams, D. C. (2016). Trends in the sand: Directional evolution in the shell shape of recessing scallops (Bivalvia: Pectinidae). *Evolution, 70*, 2061–2073.

Shimizu, H., & Namikawa, H. (2009). The body plan of the cnidarian medusa: Distinct differences in positional origins of polyp tentacles and medusa tentacles. *Evolution and Development, 11*, 619–621.

Shubin, N., Tabin, C., & Carroll, S. (2009). Deep homology and the origins of evolutionary novelty. *Nature, 457*(7231), 818–823.

Simone, L. R. L., & Amaral, V. S. d. (2008). *Plicatulostrea*, a new genus of Plicatulidae (Bivalvia: Pectinoidea) from Thailand. *The Raffles Bulletin of Zoology, 18*, 127–135.

Simone, L. R. L., Mikkelsen, P. M., & Bieler, R. (2015). Comparative anatomy of selected marine bivalves from the Florida Keys, with notes on Brazilian congeners (Mollusca: Bivalvia). *Malacologia, 58*, 1–127.

Smith, C. H., Pfeiffer, J. M., & Johnson, N. A. (2020). Comparative phylogenomics reveal complex evolution of life history strategies in a clade of bivalves with parasitic larvae (Bivalvia: Unionoida: Ambleminae). *Cladistics, 36*(5), 505–552.

Soot-Ryen, T. (1955). A report on the family Mytilidae (Pelecypoda). *Allan Hancock Pacific Expeditions, 20*, 1–175.

Stanley, S. M. (1970). Relation of shell form to life habits of the Bivalvia (Mollusca). Geological Society of America.

Stanley, S. M. (1972). Functional morphology and evolution of byssally attached bivalve mollusks. *Journal of Paleontology, 46*, 165–212.

Taylor, J. D., & Glover, E. A. (2010). Chemosymbiotic bivalves. In S. Kiel (Ed.), *The vent and seep biota* (pp. 107–135). Dordrecht: Springer.

Tëmkin, I. (2006). Morphological perspective on the classification and evolution of recent Pterioidea (Mollusca: Bivalvia). *Zoological Journal of the Linnean Society, 148*, 253–312.

Thomas, G. E., & Gruffydd, L. D. (1971). The types of escape reactions elicited in the scallop *Pecten maximus* by selected sea-star species. *Marine Biology, 10*, 87–93.

Vitonis, J. E. V. V., Zaniratto, C. P., Machado, F. M., & Passos, F. D. (2012). Comparative studies on the histology and ultrastructure of the siphons of two species of Tellinidae (Mollusca: Bivalvia) from Brazil. *Zoologia (Curitiba), 29*, 219–226.

Waller, T. R. (1976). The behavior and tentacle morphology of pteriomorphian bivalves: A motion-picture study. *Bulletin of the American Malacological Union, 1975*, 7–13.

Waller, T. R. (1978). Morphology, morphoclines and a new classification of the Pteriomorphia (Mollusca: Bivalvia). Philosophical Transactions of the Royal Society of London. *B, Biological Sciences, 284*, 345–365.

Waller, T. R. (1980). Scanning electron microscopy of shell and mantle in the order Arcoida (Mollusca: Bivalvia). *Smithsonian Contributions to Zoology, 313*, 1–58.

Wanninger, A., Koop, D., Moshel-Lynch, S., & Degnan, B. M. (2008). Molluscan evolutionary development. In W. F. Ponder & D. R. Lindberg (Eds.), *Phylogeny and evolution of the Mollusca* (pp. 1–17). Berkeley: University of California Press.

Wilkens, L. A. (2006). Neurobiology and behaviour of the scallop. In S. E. Shumway & G. J. Parsons (Eds.), *Scallops: Biology, ecology and aquaculture* (pp. 317–356). Amsterdam: Elsevier.

Yonge, C. M. (1953). Form and habit in *Pinna carnea* Gmelin. *Philosophical Transactions of the Royal Society B, 237*, 335–374.

Yonge, C. M. (1962). On the primitive significance of the byssus in the Bivalvia and its effects in evolution. *Journal of the Marine Biological Association of the United Kingdom, 42*, 113–125.

Yonge, C. M. (1968). Form and habit in species of *Malleus* (including the "hammer oysters") with comparative observations on *Isognomon isognomon*. *The Biological Bulletin, 135*, 378–405.

Yonge, C. M. (1973). Functional morphology with particular reference to hinge and ligament in *Spondylus* and *Plicatula* and a discussion on relations within the superfamily Pectinacea (Mollusca: Bivalvia). *Philosophical Transactions of the Royal Society B, 267*, 173–208.

Yonge, C. M. (1975). The status of the Plicatulidae and the Dimyidae in relation to the superfamily Pectinacea (Mollusca: Bivalvia). *Journal of Zoology, 176*, 545–553.

Yonge, C. M. (1983). Symmetries and the role of the mantle margins in the bivalve Mollusca. *Malacological Review, 16*, 1–10.