

A Hierarchical View of Convergent Evolution in Microbial Eukaryotes¹

BRIAN S. LEANDER

Canadian Institute for Advanced Research, Program in Integrated Microbial Biodiversity, Departments of Botany and Zoology, University of British Columbia, Vancouver, British Columbia, V6T 1Z4, Canada

ABSTRACT. Distinguishing convergent evolution from other causes of similarity in organisms is necessary for reconstructing phylogenetic relationships, inferring patterns of character evolution, and investigating the forces of natural selection. In contrast to animals and land plants, the pervasiveness and adaptive significance of convergent evolution in microbes has yet to be systematically explored or articulated. Convergent evolution in microbial eukaryotes, for instance, often involves very distantly related lineages with relatively limited repertoires of morphological features. These large phylogenetic distances weaken the role of ancestral developmental programs on the subsequent evolution of morphological characters, making convergent evolution between *very* distantly related lineages fundamentally different from convergent evolution between closely related lineages. This suggests that examples of convergence at different levels in the phylogenetic hierarchy offer different clues about the causes and processes of macroevolutionary diversification. Accordingly (and despite opinions to the contrary), I recognize three broad and overlapping categories of phenotypic convergence—“parallel”, “proximate” and “ultimate”—that represent either (1) subcellular analogues, (2) subcellular analogues to multicellular systems (and vice versa), or (3) multicellular analogues. Microbial eukaryotes living in planktonic environments, interstitial environments, and the intestinal environments of metazoan hosts provide compelling examples of ultimate convergence. After describing selected examples in microbial eukaryotes, I suggest some future directions needed to more fully understand the hierarchical structure of convergent evolution and the overall history of life.

Key Words. Apicomplexa, convergent evolution, dinoflagellates, gregarines, *Haplozoon*, phylogeny, *Stephanopogon*, *Strebloplastix*, tapeworm.

CONVERGENT evolution refers to the independent origin of similar organismal traits and is often the result of similar selective pressures operating in similar environments. Convergent traits have been recognized at nearly all levels of biological organization, ranging from molecules to behaviors (Emery and Clayton 2004; Zakon 2002). Distinguishing convergent evolution from other causes of similarity in organisms, such as homology and homoplasy, is necessary for interpreting the fossil record and for accurately reconstructing phylogenetic relationships (Desutter-Grandcolas et al. 2005; Rieppel and Kearney 2002). Moreover, characterizing specific examples of convergent evolution greatly improves our understanding of natural selection and macroevolution, because each example reflects a fundamental biological problem and its possible solutions (Conway-Morris 2006). Classical examples of convergent evolution have come almost exclusively from comparative analyses of animals and land plants, especially lineages that have evolved separately on different continents (e.g. different kinds of vultures and succulent plants). These examples fall within the normal range of human perspicacity and usually involve the independent evolution of relatively complex characters consisting of many different cell types and tissues, such as eyes, fins, wings, stems, leaves and flowers (Conway-Morris and Gould 1998; Donoghue 2005).

However, the overwhelming diversity and abundance of life forms on Earth consist of only one or a few cells that thrive at the microscopic scale (Oren 2004; Patterson 1999). Although microbes are often thought of as lacking significant morphological variation, this is not true even for some bacteria (Callaway 2008) and certainly not for microbial eukaryotes. The cells of free-living and parasitic microbial eukaryotes, for instance, are built from several intricate subcellular systems, such as a cytoskeleton in-

involved in locomotion and feeding, complex extrusomes involved in predation and defense, and organelles acquired by endosymbiosis (i.e. mitochondria and plastids). When characterized in detail, the known diversity of subcellular systems in microbial eukaryotes is simply staggering, and very few scientists are aware of these data. Not surprisingly, the pervasiveness and adaptive significance of convergent evolution at the subcellular level has yet to be systematically explored or articulated in a cohesive way. Doing this will inevitably reshape how we interpret the early evolution of life and how we conceptualize and analyze the seemingly intangible forces of natural selection operating at microbial scales (Purcell 1977). Improved understanding of convergent evolution in microbes will also provide a much broader framework for evaluating whether (or not) the relationship between phylogenetic distance and evolutionary convergence provides deeper insights into macroevolutionary patterns and processes (Arendt and Reznick 2008; McNamara 1990; Simpson 1952). Accordingly, this article has the following goals: (1) to popularize some major patterns of convergent evolution in microbial life forms, (2) to introduce a hierarchical view of convergent evolution that emphasizes the significance of relative phylogenetic distances, and (3) to articulate working definitions of terms that encapsulate some novel concepts.

USEFUL CONCEPTS

Terminology used in the literature to convey concepts related to the analysis of evolutionary constraint and convergence is diverse and confusing (Antonovics and van Tienderen 1991; Arendt and Reznick 2008; Desutter-Grandcolas et al. 2005; Williams and Ebach 2007), so it is necessary to first define a few relevant terms before addressing some specific examples of convergent evolution in microbial eukaryotes. For instance, familiarity with the concept of *residual capacity* or “evolutionary canalization” will enable readers to distinguish between three broad and overlapping categories of convergence: “parallel”, “proximate”, and “ultimate”. Residual capacity is the influence of ancestral constraints on subsequent evolution, and several other synonymous terms have been used in the literature to convey this concept (e.g. evolutionary potential, evolvability, latent homology, and apomorphic tendencies) (Sanderson and Hufford 1996). The concept not only refers to the genes inherited from one generation to

Corresponding Author: B. Leander, Canadian Institute for Advanced Research, Program in Integrated Microbial Biodiversity, Departments of Botany and Zoology, University of British Columbia, Vancouver, British Columbia, V6T 1Z4, Canada—Telephone number: 604-822-2474; FAX number: 604-822-6089; e-mail: bleander@interchange.ubc.ca

¹Invited presentation, part of a Joint PSA—ISOP Symposium on Symbiosis, delivered at the 58th Annual Meeting of The Society of Protistologists, convening with the Phycological Society of America, Providence, Rhode Island, August 5–9, 2007.

the next, but also the ways in which the products of those genes interact with one another, and the environment, in space and time (e.g. developmental canalization and epigenetics) (Beldade, Koops, and Brakefield 2002; Donoghue 2000; Yoon and Baum 2004).

Parallel convergence occurs over short time scales within the same environment. The convergent phenotypic characters at this scale are basically indistinguishable, reflect a strong degree of residual capacity (or developmental homology), and are nearly always discovered with robust phylogenies of relatively comprehensive taxon samples (Fig. 1a) (Hall 2003; Mueller et al. 2004; Nozaki et al. 2000; Wray 2002). However, the precise genetic mechanisms that gives rise to parallel phenotypes need not be identical; this is especially true in cases of character reduction or loss, where the modification of different genes in homologous developmental networks can lead to identical phenotypes (reviewed by Arendt and Reznick 2008).

Proximate convergence refers to analogous characters that consist mainly of homologous components (both genetic and structural) that have been modified in different ways and are sometimes referred to as “partially homologous characters” (Conway-Morris and Gould 1998). These phenotypic characters are easily distinguishable when examined closely and reflect moderate degrees of residual capacity (Fig. 1a). Some examples of proximate convergence reflect fairly straightforward genetic mechanisms, such as the independent activation (or silencing) of a key gene involved in homologous developmental programs (Hall 2003; Shapiro, Bell, & Kingsley 2006; Wray 2002). Nonetheless, most of the best understood examples of convergent evolution fall into this category, such as the streamlined bodies of sharks, tunas, ichthyosaurs and dolphins; the wings of birds, pterosaurs and bats; coloration in tropical turbellarians and nudibranchs; and the camera eyes of vertebrates and cephalopods (Donley et al. 2004; Jagger

and Sands 1999). It is significant to point out that these examples of convergent evolution are often described in the literature as involving “distantly related” lineages. However, when considering the overall evolutionary history of eukaryotes (i.e. the diversity of microbial lineages), examples of convergent evolution within specific groups, like animals or land plants, more accurately represent comparatively closely related lineages that share a great deal of homologous traits.

Ultimate convergence is a new concept that describes analogous characters consisting of very few, if any, homologous components (genetic or structural) (Fig. 1a). These characters are easily distinguishable, reflect weak residual capacity, and perhaps provide the most compelling insights about the major forces of natural selection operating on Earth. The examples outlined below offer evidence that ultimate convergence is common in microbial eukaryotes because of the relatively large phylogenetic distances that exist between different lineages of organisms with limited repertoires of morphological characters. These examples of ultimate convergence are ordered into two different sets: (1) subcellular analogues and (2) subcellular analogues to multicellular systems (and vice versa). Convergent characters in animals and land plants represent proximate multicellular analogues that have been addressed and popularized elsewhere (Arendt and Reznick 2008; Conway-Morris and Gould 1998; Donoghue 2005). Nonetheless, there is an inverse relationship between residual capacity and phylogenetic distance and the borders between parallel convergence, proximate convergence, and ultimate convergence are continuous along this slope (Fig. 1b). One of the main insights addressed here is that convergent evolution between closely related lineages (parallel convergence and proximate convergence) is fundamentally different from convergent evolution between very distantly related lineages (ultimate convergence). Therefore,

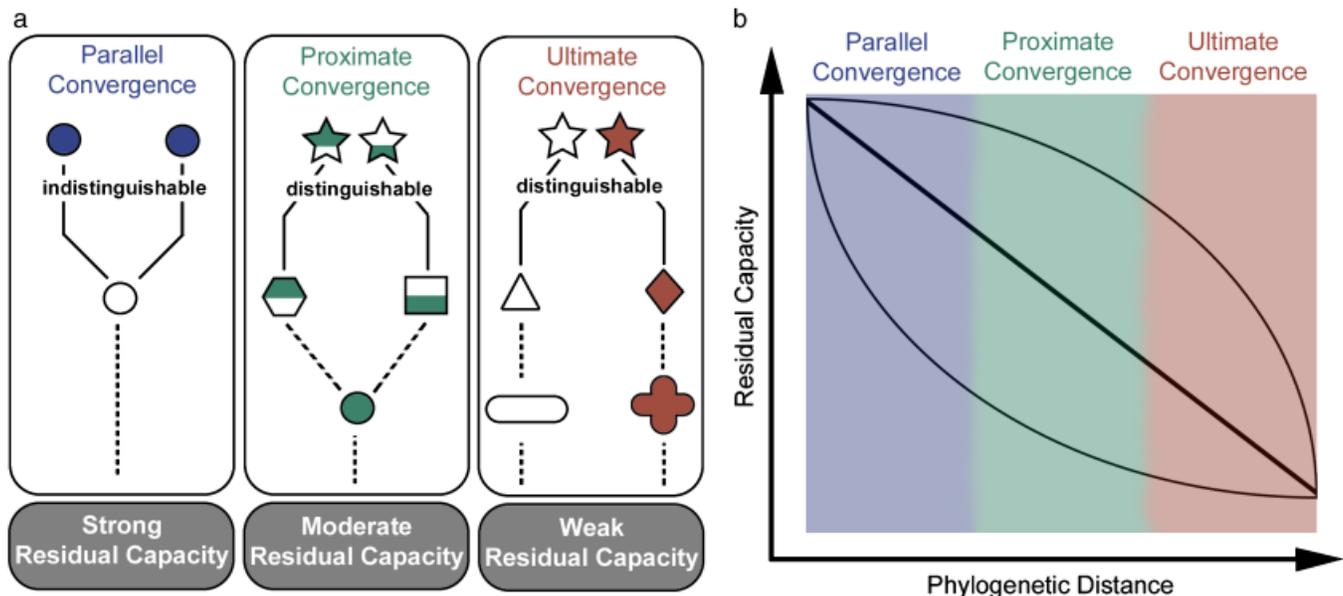


Fig. 1. Illustrations of terms that encapsulate concepts necessary for discussing convergent evolution. “Residual capacity” refers to the influence of ancestral constraints on subsequent evolution, such as developmental canalization and epigenetics. **a.** “Parallel convergence” refers to convergent characters that evolve over short time scales within the same environment. These characters are more or less indistinguishable, reflect a strong degree of residual capacity, and are discovered with robust phylogenies of relatively comprehensive taxon samples. “Proximate convergence” reflects moderate residual capacity and refers to analogous characters that consist mainly of homologous components that have been modified in different ways and are, therefore, distinguishable. “Ultimate convergence” reflects weak residual capacity and refers to analogous characters consisting of very few, if any, homologous components and are easily distinguishable. Colors and shapes represent different character states. **b.** An illustration of the inverse relationship between residual capacity and phylogenetic distance; the borders between parallel convergence, proximate convergence, and ultimate convergence are continuous along this slope. The arched lines indicate the theoretical range of residual capacities at any particular phylogenetic distance.

well understood examples of convergence at different levels in the phylogenetic hierarchy should offer different clues about the natural forces that have shaped macroevolutionary patterns.

CONVERGENT EVOLUTION IN MICROBIAL EUKARYOTES

A selection of compelling examples at the microbial scale helps substantiate the hierarchical structure of convergent evolution, and for illustrative purposes, the relative phylogenetic distances associated with each example are expressed within a modern framework of organismal relationships (Fig. 2) (Keeling et al. 2005; Parfrey et al. 2006). Microbial eukaryotes are far more diverse than is usually assumed, and several of these lineages have reached the utmost degree of morphological complexity within the confines of a single enveloping cell membrane. Lineages of free-living microbial eukaryotes, for instance, have independently evolved a wide variety of cytoskeletal extensions (e.g. flagella, axopods, and haptonemes), feeding apparatuses (e.g. rods and gullets), secreted cell coverings (e.g. scales, loricas, frustules, and spines) and intracellular armor (e.g. thecae and pellicles). The cellular complexity found in microbial eukaryotes is also magnified by endosymbiotic and ectosymbiotic relationships with bacteria and other eukaryotes. For example, mitochondria and photosynthetic plastids are the descendants of independent bacterial endosymbionts (Bhattacharya et al. 2007; Embley and Martin 2006) and can be extraordinarily diverse in morphology, even

within specific groups of closely related lineages (Triemer et al. 2006). Moreover, some modern microbial eukaryotes were formed by the amalgamation of two previously independent lineages of eukaryotes (Archibald 2005; Keeling 2004). These organisms are the manifestation of secondary and tertiary endosymbiotic events and are not only complex at the morphological level, but also the genomic level (Imanian and Keeling 2007). Therefore, when referring to the Tree of Eukaryotes (Fig. 2), it is important to distinguish clearly between the host cell lineages and the lineages from which the endosymbionts evolved.

In contrast to the endosymbiotic mode of multicellularity described above, several independent lineages of eukaryotes have increased overall body size within the microbial realm by connecting together genetically and morphologically identical copies of the ancestral cell. Examples include filament formation in planktonic diatoms and dinoflagellates, and colony formation in green algae, choanoflagellates, and chrysophytes. The repeated origins of colonial stages in choanoflagellates and green algae paved the way for the much more pronounced degrees of cellular differentiation observed in modern animals and land plants, respectively (King 2004; Kirk 2000). Moreover, many other lineages of eukaryotes have evolved outside of the microbial realm by independently increasing overall body size in very different ways: examples include the formation of coenocytic thalli in myxomycetes and some ulvophycean algae; the formation of cellular slime molds in dictyostelids; the formation of multicellular thalli in different groups of green algae, red algae, and brown

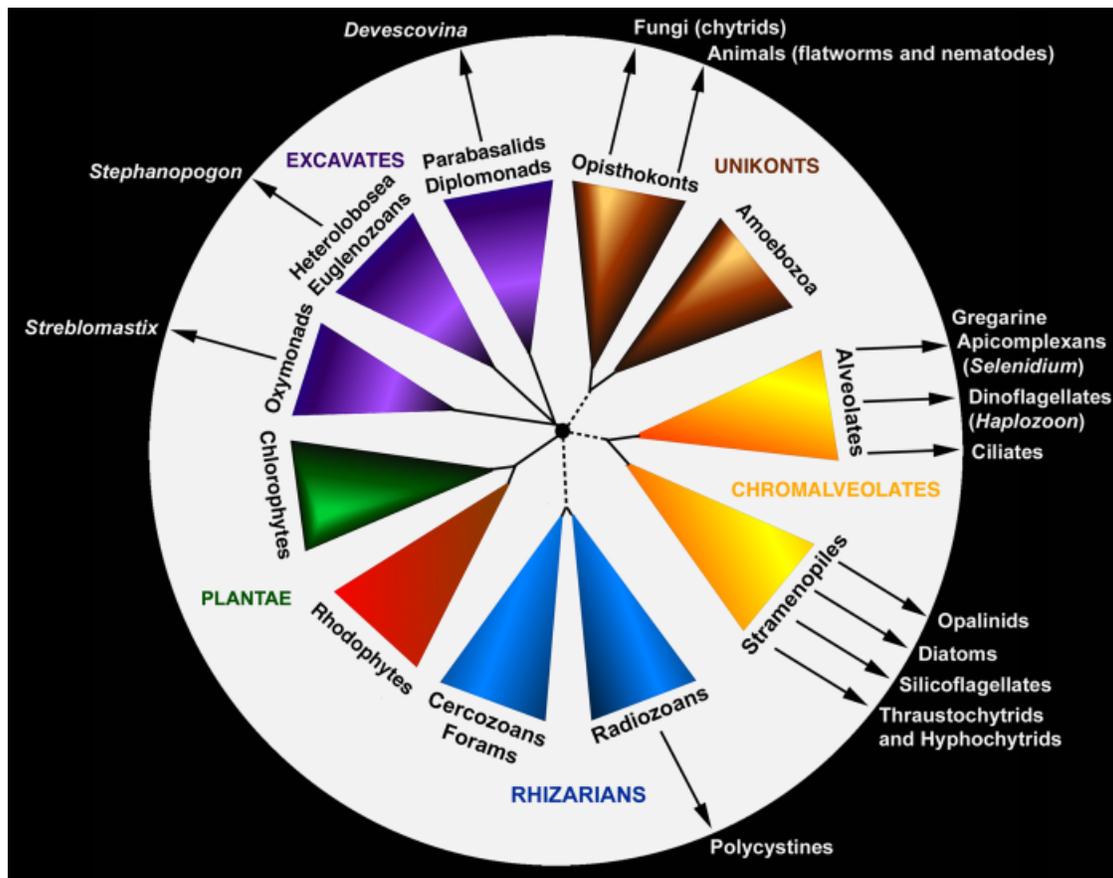


Fig. 2. An illustration of an unrooted synthetic tree depicting the phylogenetic relationships of eukaryotes based on morphological and molecular phylogenetic data. Triangles indicate diverse clades; dashed lines highlight hypothetical relationships that are currently being debated (Keeling et al. 2005; Parfrey et al. 2006). Taxa shown in white font indicate the relative phylogenetic distances associated with each example of convergent evolution discussed in this paper.

algae (e.g. *Ulva*, *Porphyra*, and *Petalonia*); and the formation of cell thread-like networks in labyrinthulids, oomycetes, and fungi. The totality of this diversification encompasses many examples of convergent evolution at different levels of the phylogenetic hierarchy, but emphasis on microbial eukaryotes is scarce. The selected examples highlighted below help rectify this situation and also further illustrate the concepts of proximate and ultimate convergence. Figure 2 is provided for reference when considering the examples discussed below.

Subcellular analogues. Examples of convergent evolution at the subcellular level are evident in very diverse ecosystems, including planktonic environments (Fig. 3a–d), interstitial environments, and the intestinal environments of metazoan hosts (Fig. 3e,f). For instance, some centric diatoms and prorocentroid dinoflagellates within marine plankton communities can look strikingly similar in overall morphology (e.g. photosynthetic ability, cell size, cell shape, and cell anatomy) (Fig. 3a,b). The basic cell structure of diatoms, however, is fundamentally different from dinoflagellates, and these lineages are only distantly related (Fig. 2). Diatoms secrete siliceous frustules that reside outside of the cell membrane (glass houses) and consist of an upper and lower valve connected by overlapping girdle bands. The valves contain numerous areolae that facilitate physiological exchanges between the cell cytoplasm and the outside environment (Fig. 3a). By contrast, dinoflagellates consist of intracellular armor composed of cellulosic plates (or thecae) that reside within alveolar sacs be-

neath the cell membrane. Like diatoms, prorocentroid dinoflagellates have evolved two large thecal plates separated by girdle bands (Fig. 3b). Several pores pierce the thecal plates in these dinoflagellates and are distributed much like the areolae in diatoms. Unlike diatoms, prorocentroid dinoflagellates also possess two flagella that are used for locomotion (not shown in Fig. 3b). The subcellular characters that make these two distantly related lineages look so similar, namely the extracellular siliceous frustules and the intracellular cellulosic plates, are not homologous at any level. This appears to be a compelling example of ultimate convergence, despite the fact that the genetic underpinnings and the selective forces responsible for these particular characters are not well understood.

Marine planktonic communities also include several distantly related lineages that have evolved radially symmetrical cells with spiny projections, such as diatoms, radiozoans, and silicoflagellates (Fig. 3c,d). Spiny projections are found in both photosynthetic and heterotrophic organisms in the plankton and have many functions that are mutually compatible, such as minimizing sinking, suspension feeding and defense against predation. Polycystine radiozoans and silicoflagellates, for instance, look very similar to one another in superficial morphology, but are fundamentally different in cell structure. Polycystines are heterotrophic (although they often harbor photosynthetic endosymbionts) and form solid silica within the cell, whereas silicoflagellates are photosynthetic and secrete solid siliceous spines outside of the cell.

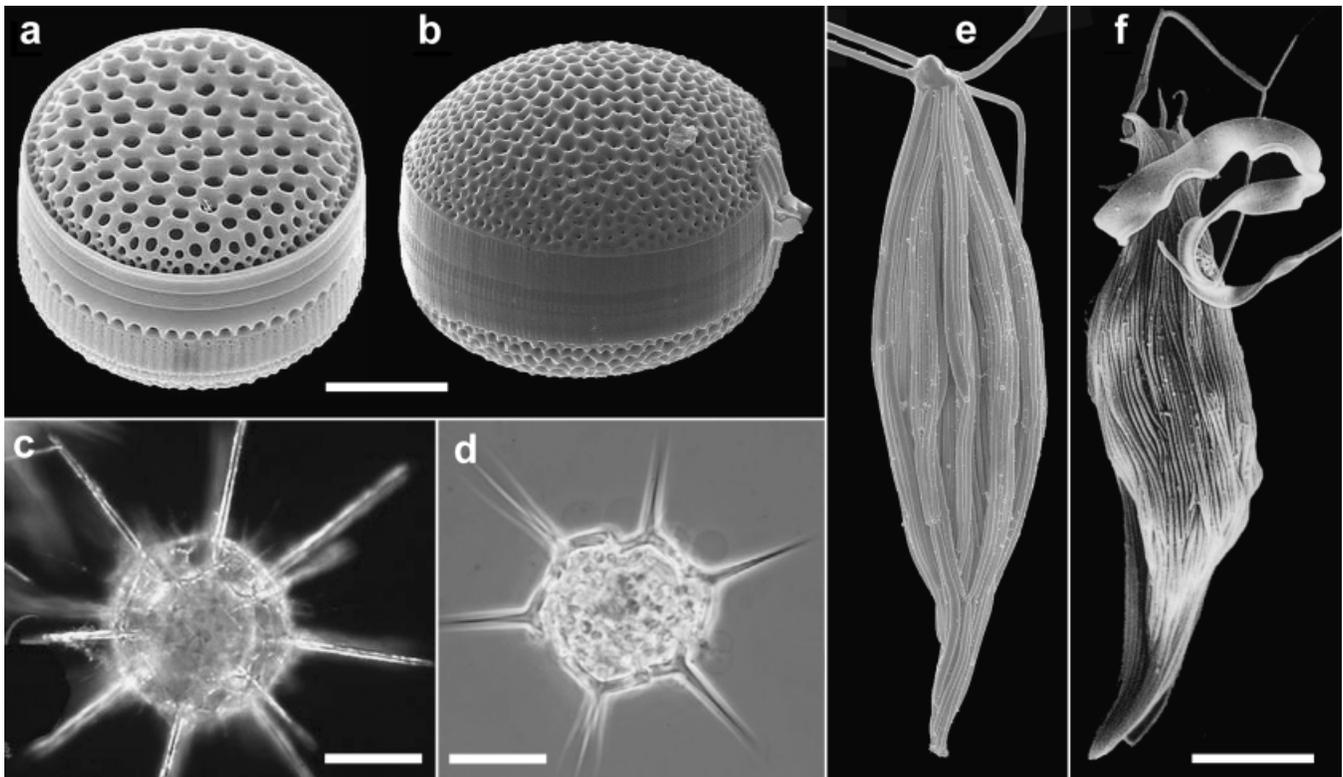


Fig. 3. Examples of proximate and ultimate convergent evolution of subcellular systems in microbial eukaryotes. These examples include organisms that inhabit marine planktonic environments (a–d), and microaerophilic intestinal environments (e, f). **a.** Scanning electron micrograph (SEM) of a centric diatom. **b.** SEM of a prorocentroid dinoflagellate, *Prorocentrum* (Bar = 10 μ m). **c.** Light micrograph (LM) of a polycystine radiozoan (Bar = 20 μ m). **d.** LM of a silicoflagellate, *Dictyocha* (Bar = 10 μ m). **e.** SEM of an oxymonad, *Streblomastix*, collected from the hindgut of the damp-wood termite, *Zootermopsis*. **f.** SEM of a parabasalid, *Devescovina*, collected from the hindgut of dry-wood termite, *Cryptotermes* (Bar = 5 μ m). The organisms shown in (e, f) highlight convergent evolution of characters associated with symbiotic relationships between ectobiotic bacteria and eukaryotic hosts. Relative phylogenetic distances between these examples are shown in Fig. 2. **b.** Reproduced with permission, from M. A. Faust; **c.** reproduced, with permission, from Image Quest Marine; **d.** reproduced under license from <http://microscope.mbl.edu> and with permission from D. Patterson; **a.** reproduced, with permission, from Leander and Keeling (2004); **f.** reproduced, with permission, from Brugerolle and Lee (2000).

The formation of biomineralized skeletons, such as solid silica, has occurred many times independently in marine eukaryotes (e.g. ebrriids, thaumatomonads, diatoms, actiniscid dinoflagellates, and poriferans) and ecophysiological explanations for this phenomenon have been summarized elsewhere (Knoll 2003). Although the independent origin of siliceous spines in very distantly related lineages appears to represent ultimate convergence, it is possible that homologous genes inherited from a very distant common ancestor are involved in the formation of solid silica in these unrelated subcellular structures. If so, then these examples might sit on the imprecise boundary between ultimate and proximate convergence (Fig 1b).

A compelling example of proximate convergence at the subcellular level involves characters associated with episymbiotic relationships with bacteria in low-oxygen environments (Fig. 3e,f). Many oxymonads and parabasalids, for instance, thrive within the hindguts of wood eating insects and play critical roles in the host's ability to extract nutrients from the ingestion of cellulose. Molecular phylogenetic evidence indicates that both lineages co-evolved with insects independently from different free-living ancestors. Some oxymonads and parabasalids are spindle-shaped cells that are completely covered in elongated episymbiotic bacteria (Fig. 3e,f), and it is clear that neither the cell shape nor the episymbionts were inherited from the most recent common ancestor of these two eukaryotic lineages. Moreover, both oxymonads and parabasalids independently acquired a motile microtubular axostyle that runs through the longitudinal axis of the cell (Simpson 2003). Although the functional significance of the axostyle and the bacterial episymbionts is unclear, the relatively close relationship between oxymonads and parabasalids within the Excavata suggests that these features reflect homologous genetic capacities that have been co-opted in similar but independent ways.

Another example of subcellular analogues involves striking similarities in flagellar patterns on the cell surface of three very

distantly related lineages, namely ciliates, opalinids, and *Stephanopogon* (Fig. 2, 4a–c) (Kostka et al. 2004; Lipscomb and Corliss 1982; Yubuki and Leander 2008). Each of these lineages evolved from different biflagellated ancestors through the independent multiplication of the flagellar apparatus. These arrays of short flagella (or cilia) enhance at least two compatible functions: locomotion and increased cell surface area. Many ciliates and *Stephanopogon*, for instance, are voracious predators of other microbial eukaryotes living at the substrate-water interface and within the spaces between sand grains. Coordinated movements of the longitudinal arrays of flagella enable these microbial predators to navigate through interstitial environments with sophistication and precision. By contrast, some ciliates and opalinids are either parasites or endocommensals of metazoan hosts, such as fish and frogs. Longitudinal arrays of flagella create surface area and microcurrents needed to acquire food within nutrient-rich environments, such as the intestinal lumina of animals. Other lineages of microbial eukaryotes, such as hypermastigote parabasalids, have also adapted to intestinal environments several times independently by multiplying the flagellar apparatus in different ways. Nonetheless, although some ciliates, opalinids, and *Stephanopogon* look similar at a superficial level (Fig. 4a–c), these cells are fundamentally different in nearly every other aspect (e.g. mitochondrial cristae, nuclei, and cytoskeletal organization), which reflects the large molecular phylogenetic distances between them. Therefore, the analogous patterns of homologous flagella in these very distantly related lineages of microbial eukaryotes represent examples of proximate convergence that approach the conceptual boundary of ultimate convergence (Fig 1b).

Subcellular analogues to multicellular systems (and vice versa). Ultimate convergence refers to analogous characters that lack homologous subcomponents. Perhaps the most compelling examples of ultimate convergence involve comparative analyses of intestinal parasites and the discovery of subcellular analogs to multicellular systems. For instance, adult tapeworms are particu-

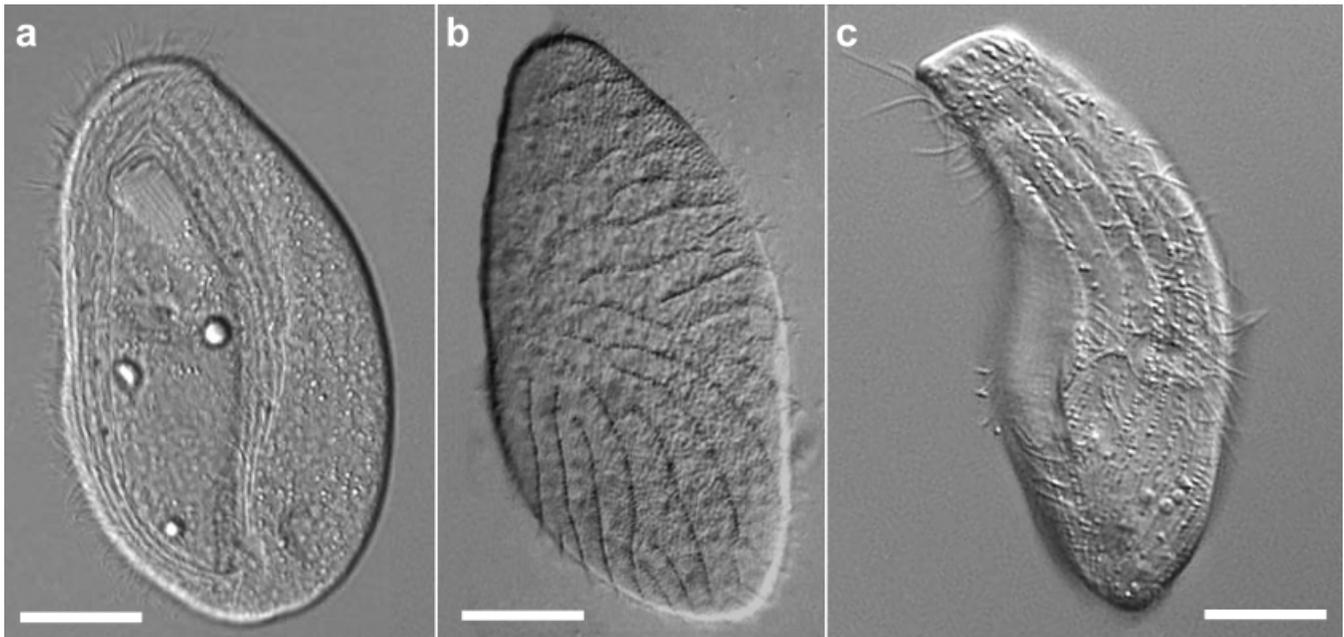
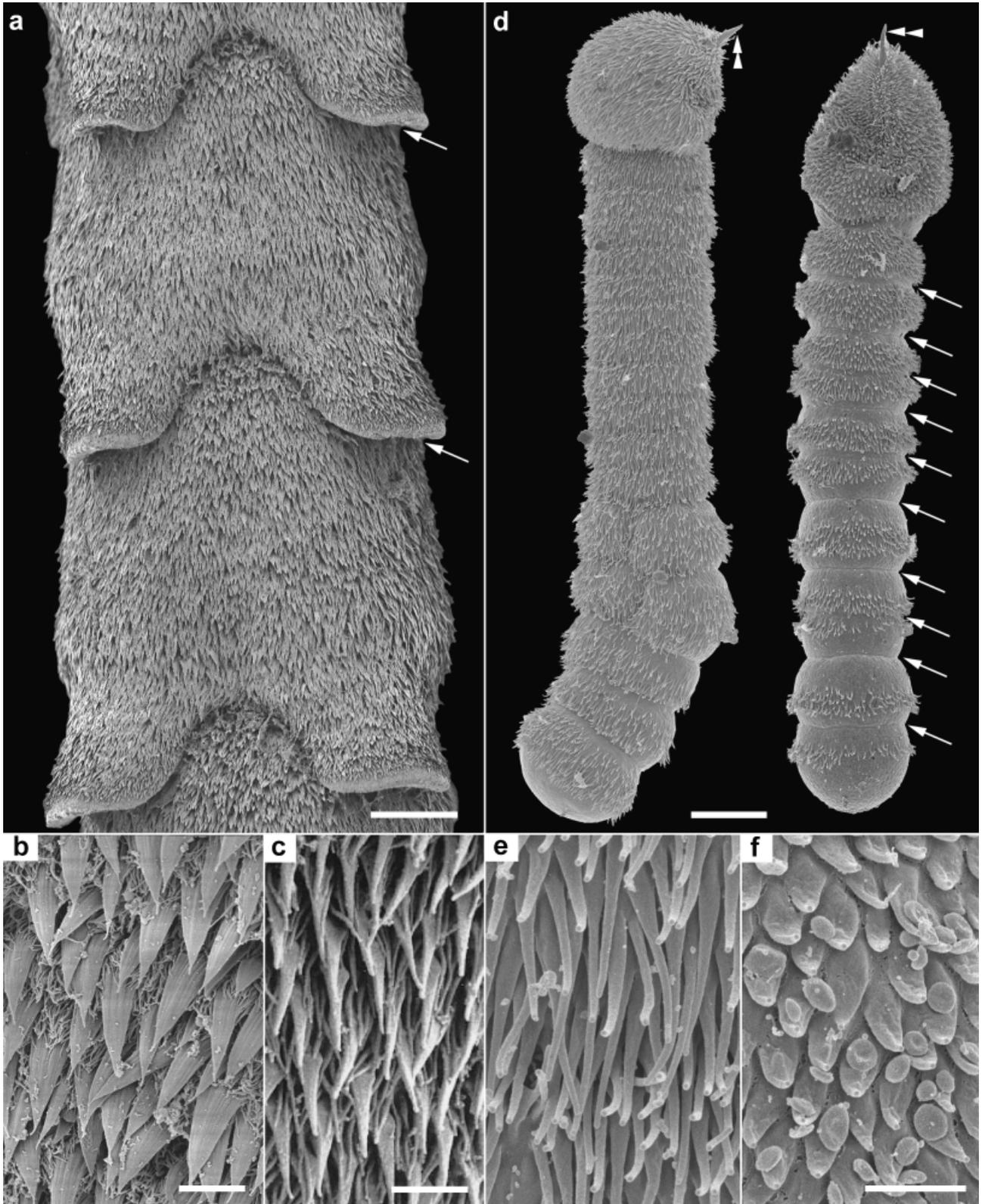


Fig. 4. Examples of proximate convergent evolution of subcellular systems in microbial eukaryotes. **a.** Light micrograph (LM) of a parasitic ciliate of fish, *Chilodonella*, showing linear rows of short flagella (bar = 10 μ m). **b.** LM of a parasitic stramenopile of frogs, *Opalina*, showing linear rows of short flagella (bar = 10 μ m). **c.** LM of a marine interstitial eukaryovore, *Stephanopogon*, showing linear rows of short flagella (bar = 15 μ m). Relative phylogenetic distances between these examples are shown in Fig. 2. A–C. reproduced under license from <http://microscope.mbl.edu> and with permission from D. Patterson.

larly well adapted to intestinal environments and consist of a strobilized system of flattened proglottids. The scolex, or the attachment end of tapeworms, is relatively tiny and usually consists

of suckers (acetabula) and hooks (rostellum). New proglottids are generated and sequentially added to the strobila in the neck region just behind the scolex. As the proglottids mature, their position



gradually shifts to the posterior end of the strobila. The posterior-most proglottids are reproductively mature and eventually detach from the strobila and leave the host with the feces in order to complete the life cycle. Each proglottid is anatomically equivalent to an individual (free-living or ectoparasitic) flatworm, so the strobila is fundamentally a string of identical units with complete hermaphroditic reproductive systems, muscles, and excretory ducts (Fig. 5a, 6a). Because tapeworms are surrounded by nutrients within the host intestines, each proglottid lacks an internal digestive system and instead uses their tegument to acquire nutrients. For this reason, tapeworms are sometimes considered parasites that have been turned inside out. Nonetheless, the syncytial tegument of proglottids in many tapeworms is adorned with dense arrays of microtrichs that are pointed toward the posterior end of the strobila (Fig. 5a–c). The microtrichs create surface area and are thought to facilitate the generation of microcurrents that enhance nutrient acquisition within the intestines. Thus, the strobilized body plan of tapeworms consists of a chain of multicellular systems—the scolex and proglottids—each constructed from different tissues and cell types.

Several poorly known lineages of single-celled parasites also inhabit the intestinal tracts of metazoan hosts and have converged on many of the features in tapeworms described above. These enigmatic examples offer compelling evidence for ultimate convergence involving subcellular analogues to multicellular systems. For instance, dinoflagellates in the genus *Haplozoon* have become highly specialized parasites within the intestines of malidanid polychaetes. Like tapeworms, haplozoans have become strobilized and consist of an attachment end called the trophocyte, followed by a chain of gonocytes and terminal sporocytes (Fig. 5d) (Leander, Saldarriaga, and Keeling 2002; Siebert and West 1974). Like the scolex of tapeworms, the trophocyte of haplozoans consists of a ventral sucker and motile stylets that are analogous to the hooks of tapeworms and that enable the parasite to attach to the intestinal lining of the host. New gonocytes are generated near the neck of the trophocyte, and the most mature units in the strobila are the sporocytes positioned at the posterior end. Like mature proglottids, the sporocytes eventually detach from the posterior end of the strobila and leave the host via the feces in order to complete the life cycle (Shumway 1924). The strobila of haplozoans is completely enveloped by a continuous cell membrane and the units are separated by internal compartmentalization of alveolar membranes. Each alveolar sac that is situated beneath the cell outer membrane contains a thecal plate that forms a barb directed posteriorly (Fig. 5d–f). The thecal barbs of haplozoans are nearly identical in morphology and density to the microtrichs of tapeworms and almost certainly provide the same functional advantages within the intestines (Fig. 5). Dinoflagellates and tapeworms are about as distantly related as any two eukaryotic lineages could be (Fig. 2), and the fundamental difference between them is that haplozoans consists of one single compartmentalized

cell and tapeworms consist of integrated multicellular tissues. Therefore, the analogous characters—strobilization, surface barbs, and attachment structures—do not contain any homologous subcomponents, which makes this an excellent example of ultimate convergence.

Similarities in metazoans and different lineages of marine gregarine apicomplexans also offer compelling examples of ultimate convergence involving subcellular analogues to multicellular systems (Fig. 2). For instance, the individual proglottids of tapeworms are similar to single-celled apicomplexan parasites, namely *Selenidium vivax*, that inhabit the intestines of peanut worms (Fig. 6a–d). Like proglottids, the trophozoites of *S. vivax* are highly motile and increase surface area by being greatly flattened. The peristaltic-like motility observed in proglottids is facilitated by different layers of muscle oriented in different directions; whereas, the peristaltic-like motility in *S. vivax* is produced by different clusters of microtubules oriented in different directions (Leander 2006). Likewise, some marine gregarine apicomplexans (e.g. *Selenidium* species) and many nematodes are fundamentally similar in both form and behavior (Fig. 6e–h). The sinusoidal motility in nematodes, for instance, is produced by bundles of longitudinal muscle that work antagonistically against an elastic cuticle (Fig. 6f); whereas, the sinusoidal motility in many *Selenidium* species is produced by longitudinal microtubules that work antagonistically against a tri-layered inner membrane complex (Fig. 6f). Therefore, the configuration of microtubules and overall cell structure in some *Selenidium* species represent subcellular analogues to the configuration of multicellular tissues present in nematodes and tapeworms (Fig. 6). Both of these examples offer compelling evidence for ultimate convergence.

As should probably be expected, the distinction between ultimate and proximate convergence is not always straightforward, even when comparing subcellular analogues to multicellular systems. For instance, both the proglottids of tapeworms and the trophozoites of *S. vivax* have dense accumulations of mitochondria positioned immediately below the surface (Fig. 6b, d). The superficial distribution of mitochondria in these independent lineages is functionally related to the low amount of oxygen found within the intestinal lumen and is presumably advantageous for localizing the chemical energy needed for motility and surface-mediated nutrition. On one hand, because mitochondria are homologous in all eukaryotes, the analogous distribution of mitochondria in tapeworms and *S. vivax* is consistent with the concept of proximate convergence (independent modification of homologous components). On the other hand, the exceedingly large phylogenetic distance between apicomplexans and metazoans is most consistent with the concept of ultimate convergence (Fig. 2). Therefore, debating the categorical limits for some examples is insignificant when compared with the realization that convergent evolution can take place between very distantly related lineages with fundamentally different body constructions.

Fig. 5. Examples of ultimate convergent evolution—subcellular analogues to multicellular systems in *Haplozoon* dinoflagellates and tapeworms. **a.** Scanning electron micrograph (SEM) showing the surface microtrichs on the proglottids of a tapeworm, *Anthobothrium*, collected from the intestines of a blue shark. The proglottids are connected together (arrows) along the length of the strobila (Bar = 20 μ m). **b, c.** High magnification SEMs of tapeworm microtrichs, the posterior end of the strobila is toward the bottom (Bars = 2 μ m). **d.** SEMs showing the strobilized morphology of *Haplozoon axiothellae* (Dinoflagellata) isolated from the intestines of a malidanid polychaete. Two individual parasites from the same host are presented in different orientations: right lateral view (left) and ventral view (right). The anterior-most trophocyte consists of a ventral sucker and motile stylets (double arrowheads) and is followed by a chain of gonocytes and posterior sporocytes that are delimited by constrictions in the cell membrane (arrows) (Bar = 10 μ m). **e, f.** High magnification SEMs of microtrich-like thecal barbs on the surface of *Haplozoon*. The posterior end of the strobila is toward the bottom (Bar = 1.5 μ m). Relative phylogenetic distances between these examples are shown in Fig. 2. A–C. provided by J. Caira (University of Connecticut, USA); D–F. reproduced, with permission, from Ref. Leander et al. (2002).

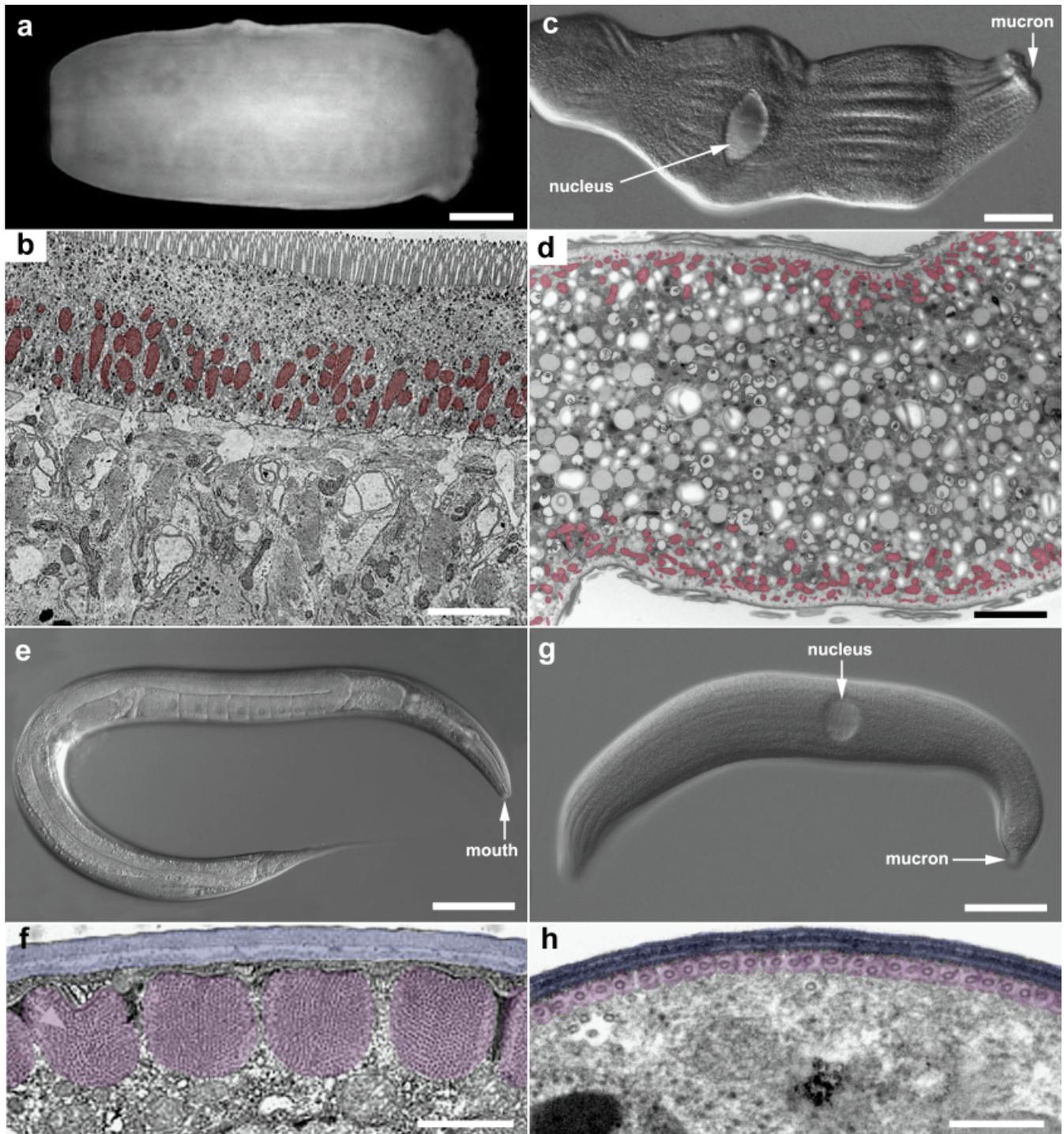


Fig. 6. Examples of ultimate convergent evolution—subcellular analogs to multicellular systems in intestinal parasites. **a.** Light micrograph (LM) of an individual proglottid of a tapeworm (Bar = 30 μm). **b.** Transmission electron micrograph (TEM) of a tapeworm showing a superficial accumulation of mitochondria (red) in the tegument (Bar = 4 μm). **c.** LM of a marine gregarine apicomplexan, *Selenidium vivax*, isolated from the intestines of a peanut worm (Bar = 20 μm). **d.** TEM of *S. vivax* showing a superficial accumulation of mitochondria (red) in the large flattened cell (Bar = 4 μm). **e.** LM of a nematode, *Caenorhabditis briggsae*. **f.** TEM of *C. elegans* showing bundles of longitudinal muscle (purple) subtending an elastic cuticle (blue) (Bar = 10 μm). **g.** LM of marine gregarine apicomplexan, *Selenidium serpulae* isolated from the intestines of a calcareous tubeworm (Bar = 15 μm). **h.** TEM of *S. serpulae* showing a row of longitudinal microtubules (purple) subtending an elastic, tri-layered inner-membrane complex (blue) (Bar = 0.2 μm). Relative phylogenetic distances between these examples are shown in Fig. 2. **b.** Reproduced with permission from Lumsden (1975); **c,d.** reproduced with permission from Leander (2006); **f.** reproduced from Herndon et al. (2002); **g, h.** reproduced, with permission, from Leander (2007).

CONCLUSIONS AND FUTURE DIRECTIONS

The pervasiveness and adaptive significance of convergent evolution at the microbial scale is only just beginning to be explored and characterized. Nonetheless, it is clear that examples of convergent evolution in microbial eukaryotes help demonstrate the significance of phylogenetic distance, and the corresponding residual capacities, in distinguishing between parallel convergence, proximate convergence, and ultimate convergence. Although these sub-phenomena of convergent evolution represent zones along a continuum, they are discernible based on the relative degree of homology present in the traits of interest. Examples of parallel convergence and proximate convergence, for instance, are common across all eukaryotes and are particularly well known in animals and land plants. The most compelling examples of ultimate convergence include subcellular analogues in free-living microbial eukaryotes and subcellular analogues to multicellular systems in intestinal parasites. Therefore, different examples of convergent evolution reflect different levels in the phylogenetic hierarchy and offer different insights about the mechanisms that underpin broad patterns of morphological change and the selective forces operating on Earth. Accordingly, a more complete understanding of the hierarchical structure of convergent evolution and the overall history of life will require further advancement in the following research areas: (1) describing the overall diversity of microbial life, (2) reconstructing the Tree of Eukaryotes by establishing robust internal phylogenies for major eukaryotic groups, (3) experimentally demonstrating the selective forces operating at microbial scales within functional and ecological contexts, and (4) characterizing the patterns and processes associated with the development of complex subcellular systems in eukaryotic cells.

ACKNOWLEDGMENTS

This work was supported by grants from the Tula Foundation (Centre for Microbial Diversity and Evolution), the National Science and Engineering Research Council of Canada (NSERC 283091-04), and the Canadian Institute for Advanced Research, Program in Integrated Microbial Biodiversity. I wish to thank David Patterson, Janine Caira, and Maria Faust for providing Fig. 3d, 4a–c; Fig. 5a–c; and Fig. 3b, respectively.

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Received: 11/27/07, 01/15/08; accepted: 01/06/08