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Appendix A

Definition of Ecospace Characters

This appendix presents and defines each of the ecological characters and character states in the ecospace framework, including discussion of examples, exceptions, and problematical issues. The following descriptions are not intended to offer a rationale for choosing each autecological character or to define common terms; rather, they justify how the various characters should be coded operationally and provide examples to explain their broad usage. Information available in introductory textbooks covering organismal ecology (e.g., Campbell and Reece 2004; Raven et al. 2004; Brusca and Brusca 2002) is not individually cited. Several of the terms are new or adapted from specific disciplines; these are defined. Several are in common usage (Lincoln et al. 1992) and are discussed only to note deviations from existing definitions. Neutral terminology is used whenever possible to keep jargon to a minimum. Characters set in parentheses are expected to be useful for future applications, but are not expected for immediate utility in studies including fossils. The ecospace framework as currently described here includes 27 characters (in bold) and 60 character states (numbered and italicized). The character brooding with a single alternative—present or absent—is treated as both a character and a character state. Unless noted, the term *individuals* in the following refers to individual ecological entities—individuals or species—while the term *groups* refers to more inclusive groups—communities and lineages.

Binary characters—Each of these characters is coded as 0 for absent and 1 for present, unless noted.

Reproduction—The reproductive mode of the individual. It is possible to be both sexual and asexual, whether via hermaphroditism (whether protandrous, protogynous, synchronous, or sequential), via periodic sexual reversal or parthenogenesis, or via having both asexual budding and sexual processes.

1. *Sexual*—Those individuals that reproduce sexually, whether individuation of offspring occurs or not.
2. *Asexual/Clonal*—Those genetically identical (barring mutation) individuals that reproduce asexually via fission, budding, or cloning, and that originate from a single individual (i.e., an ortet). Note that asexual individuals are defined solely by reproductive mode and not by the act of forming colonies, although such correlation may be common. Individuals that can regenerate portions of their body are not included here unless such capabilities regularly lead to fission or other reproductive processes.

(Development)—The mode of reproductive development for an individual. For marine invertebrates, this character is typically correlated with geographic and dispersal range (Jablonski and Lutz 1983; Jablonski 1986; Brown 1995). This character includes all aspects of development, whether larval development, insect metamorphosis, or plant alternation of generations. Not included is dormancy that occurs within an individual's lifetime and that is not directly related to reproductive development. In cases where individuals begin development as a lecithotrophic larva, becoming planktotrophic prior to settlement, it is appropriate to categorize the individual as both lecithotrophic and planktotrophic. Multiple character states can also apply when a species is developmentally plastic or can switch developmental strategies as a function of environmental condition.

3. *Direct development*—Direct-developing individuals, with or without brooding and with or without eggs, in which offspring are capable of self-sufficiency (barring sexual maturation) and resemble miniaturized adults (barring minor allometric growth). Among insects, only ametabolous and hemimetabolous individuals are included in this character state.
4. *Indirect, non-feeding development*—Indirect-developing individuals (i.e., undergoing one or more life stages), with or without brooding and with or without eggs, in which offspring are sustained by yolk or other physically attached nutriment after birth. By this definition, all seed plants would be included in this character state.
5. *Indirect, feeding development*—Indirect-developing individuals (i.e., undergoing one or more life stages), with or without brooding and with or without eggs, in which offspring are capable of feeding self-sufficiently after birth. Holometabolous insects, spore-bearing plants, fungi, and slime molds are generally included in this character state.

6. **(Brooding)**—Individuals for which brooding, encapsulation, or any other form of post-birthing, direct parental process is involved with reproduction. Incubation, protection, and cultural transmission (teaching) are all included in this character state. Brooding can occur for both direct- and indirect-developing individuals. Common brooders include many mammals, birds, dinosaurs (Horner 2000), ostracodes and other crustaceans, and possibly some trilobites (Fortey and Hughes 1998).

(Dispersal vector)—The primary means by which larvae, spores, fertilized eggs, seeds, or other offspring (whether sexual or asexual) undergo dispersion. Dispersal can occur for both direct- and indirect-developing individuals. Although passive methods (states 8, 9) often involve the presence of structural or behavioral adaptations for dispersion, they are considered passive because they are not capable of self-sufficient dispersion. In the case of larvae with ciliary locomotion, the choice of character state depends on the relative efficacy of active locomotion versus passive dispersal. Multiple character states are possible, although emphasis is on the primary means of dispersal.

7. *No vector*—No dispersal vector is involved; offspring remain in the same location as the parent.
8. *Fluid-dispersed*—Offspring are entrained by wind or water currents and are transported passively.
9. *Organism-dispersed*—Offspring adhere to some organismal vector and are transported passively. This includes plants attached to animals as well as planktonic larvae attached to floating plants, algae, or animals (pleuston).
10. *Self-dispersed*—Offspring disperse actively via self-sufficient migration.

Mobility—The ability of an individual to move within its environment, regardless of any energy expended in such effort. These character states are tallied as binary because there is no unambiguous scale by which to logically order them. As above, passive methods do not denote the lack of structural or behavioral adaptations involved in mobility.

11. *Sedentary*—Immobile individuals, independent of attachment to substrate. These individuals will not change location even if disturbed, whether because of permanent attachment or inability to move. It also includes animals that move in place, such as pedunculate brachiopods that use muscular contractions to maintain orientation at sediment surface, to face feeding currents, and to shake off fouling individuals (Richardson and Watson 1975a,b; Richardson 1981). Note that this definition is modified from the more typical use of this term that often implies attachment. The term *sessile* has been avoided because of its dual connotation of immobility and attachment.
12. *Passively mobile*—Mobile individuals, but relying primarily on ambient flow for motion. This includes planktonic individuals that have some form of ciliary or buoyancy control

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over depth stratification or orientations, but whose activities are insufficient to move against typical currents. In the aquatic realm, this encompasses planktonic individuals and occasional benthic epibionts, such as the bivalve *Pteria* attached to the upper arms of octocorralian corals (Stanley 1970). Terrestrial examples include tumbleweed; aerial examples include some insects, and the dispersal stages of many taxa(if such life stages are coded separately). Some deep-water pycnogonid chelicerates also would be included in this character state (Brusca and Brusca 2002).

13. *Facultatively mobile*—Individuals that are capable of mobility, but are typically immobile. Common examples include the inarticulate brachiopod *Lingula*, many byssate bivalves, and the deep-burrowing, pholadomyoid bivalves that can re-burrow when disturbed.
14. *Intermittently mobile*—Individuals that move about throughout their life, but that often remain in one location for appreciable durations. In most cases, mobility is associated with a change in feeding location. Common examples include tubicolous spionid and onuphid polychaetes and deposit-feeding tellinid bivalves, which remain in one location for extended periods, moving when local nutrition is depleted (Fauchald and Jumars 1979; Stanley 1970). This character state also includes generally sedentary individuals that limit movement to diurnal cycles, such as comatulid crinoids that move nocturnally from reef crevices to reef crests to feed and remain sedentary throughout the night (Meyer 1973). This character state is equivalent to the term ''discretely motile'' used by Fauchald and Jumars (1979) in classifying polychaetes.
15. *Habitually mobile*—Individuals that are primarily mobile (or vagile), although able to rest periodically. This vagility is independent of the medium in which motion occurs; thus, reptant (crawling on substrates), ambulatory (walking), cursorial (running), natant (swimming), burrowing, and flying individuals are all included here. This character state also includes individuals that rest within fluids (e.g., nektonic and demersal aquatic individuals and gliding aerial animals) as well as those that rest on substrates (e.g., aquatic nektobenthos). The distance moved is not a factor here; habitually mobile individuals that move freely, but within a spatially restricted domicile or trap (such as web-building and trapdoor spiders), are still habitually mobile.

Substrate/medium composition—The composition of an adult individual's *immediate* substrate, whether attached to it or not. This character does not refer to the composition of the overall habitat; for example, individuals may attach immediately to shelled animals or algae within an overall liquefied chalk (Surlyk 1972). It also does not refer to the substrate of juvenile individuals, which may differ from that of adults (unless such life stages are coded separately). Only in cases where a substrate is not involved, such as involving plankton or nekton, should this character refer to the surrounding medium. There may not always be an unambiguous distinction between the biotic and lithic character states when referring to biogenic sediments and structures, such as calcarenites, oncoids, coals, rudites (reef stones), algal boundstones, and stromatolites (Taylor and Wilson 2002). When organisms do not make a substrate distinction between the shells of living organisms and fully degraded shell debris, coding both states may be appropriate. Many individuals, such as barnacles, are substrate generalists that can inhabit multiple substrates, whereas other individuals can have multiple substrates simultaneously. An example of the latter are many plants—especially lianas—that root into a soft, lithic soil, but support themselves in the forest canopy with tendrils around hard, biotic substrates (Givnish and Vermeij 1976; Putz 1984). This character is independent of the consistency of the substrate (see character states 19–21 below).

16. *Biotic*—Substrate consists of either living or recently dead, tissular or skeletal medium. This character state includes resting on or against another individual (e.g., the clinging, arboreal, epibiotic, and ectoparasitic habits) as well as active erosion (e.g., the boring habit), excavation (e.g., the mining habit), penetration (e.g., the endoparasitic habit), and passive entombment by the surrounding individual (e.g., the nestling habit).
17. *Lithic*—Substrate consists of chemically precipitated or physically eroded sediment, rock, soil, or other inorganic medium, regardless of whether microbial agents or other individuals were involved in the genesis of such material. This character state includes individuals that burrow within sediment, that live interstitially among sediment grains, that live within individual rocks, or that lie upon such substrates (e.g., the epibenthic habit). Long-dead shell debris, wood, algal mats, and other biogenic sediments and structures should only be included in this state when such material has been diagenetically altered and the organic fraction has been decomposed and leeched.
18. *Fluidic*—The enclosing medium is primarily water (e.g., the pelagic or nektic habit) or air (e.g., the aerial, or atmobiotic, habit), although the individual may occasionally rest against other substrates (e.g., the nektobenthic and demersal habits). This character state also includes those neustonic individuals, such as water gliders, whose substrate itself is water.
19. *Insubstantial*—Flying, swimming, and planktonic individuals whose surrounding medium is a fluid and therefore lacks consistency.

Substrate consistency—The firmness of an adult individual's immediate substrate, whether attached to it or not. As above, this character does not refer to the composition of the overall habitat or to the substrate of juveniles. This character is independent of the composition and elasticity of the substrate. A general guideline is whether an individual is able to penetrate the substrate without resorting to active excavation. For example, oligochaetes and plant roots that push through soils occupy a soft substrate, whereas insects that live on the surface of leaves or on the surface of water occupy a hard substrate. Note also that this character is scale dependent: a sandy substrate may be soft for benthic gastropods and hard for interstitial hydroids. Parasites will follow similar codings, often with ectoparasites (and gastrointestinal endoparasites) on hard, epithelial integument, and interstitial endoparasites in soft tissue. Multiple states are possible for the same species as well as for the same individual (see note on climbing plants in prior character, substrate/medium composition.)

20. *Soft*—Individuals whose immediate substrate is soft, including disaggregated, soupy, thixotrophic, and unconsolidated sediments or soil.
21. *Hard*—Individuals whose immediate substrate is firm, including lithified, consolidated, or cemented sediments; caliche soil; shells, other skeletons, or other firm individuals; and the air-water interface, depending on the individual. For example, the water surface is a durable and impermeable substrate for water glider insects, but an insubstantial one for flying fish.

Substrate relationship—The relationship between an adult individual and its *immediate* substrate. Note that this character is independent of the nature of the substrate and an individual's ability to move against or among its substrates.

22. *Attached*—Adult individuals that are physically attached to their immediate substrate, regardless of whether such at-

tachment is permanent and whether the attachment penetrates the substrate. For example, some tubicolous polychaetes and other individuals that construct tubes admixed with adjacent sediments are effectively attached, even though such individuals are occasionally able to relocate to additional domiciles (Fauchald and Jumars 1979). Excluded from this attached habit are those individuals, including many amphipods, that create tubes or other structures, that use a tube only for a stable domicile, that move about with their tubes, and that are otherwise free-living. Attachment can apply equally to individuals attached along their entire body surface (e.g., the adnate habit of encrusting individuals) as well as those attached only by an appendage or portion of the body (e.g., the tethered habit). Forms of attachment include rooting (the rhizomenal habit) as well as cementation, suction, clasping, clinging, or other ephaptomenal habits. Note that most colonial animals are attached, even if the attachment is of living individuals (whether zooaria, polyps, etc.) to the dead skeletons of prior generations. If coded from the perspective of adult individuals, attachment does not include those that are attached as juveniles but become free-living as adults (e.g., the liberosessile habit of Bassett 1984).

23. *Free-living*—Adult individuals that are free-living (the planomenal habit) and that are not attached in any permanent or semi-permanent manner to substrates, regardless of their mobility. The free-living habit includes those individuals that never come in contact with substrates as well as those individuals that rest on substrates.

Primary microhabitat—The maximum typical resting location (or perching height) of an individual with regard to the *primary* substrate of the focal habitat. This character does not refer to the microhabitat in which food is acquired (see character states 30–33 below), nor to the maximum distance away from the substrate that the individual is capable of moving, unless such distances coincide with the typical resting position.

The primary substrate is dependent on the habitat being studied. For aquatic communities, this substrate will generally be the sediment-water interface; for terrestrial and aerial communities, it is the ground; for neustonic communities, it is the air-water interface; and for parasitic communities, it is the host's epithelium or appropriate tissular layer. Problems arise when considering those habitats lacking an obvious substrate. For practicality, atmobiotic and pelagic communities should be classified in relation to the closest ground and/or air-water interface; because few individuals are capable of living at the outer envelope of the atmosphere, this decision is obvious for atmobiotic communities. However, pelagic communities should be classified according to the focus of the study. If the focus is on marine epipelagic or lacustrine littoral-depth communities, then the appropriate substrate is the air-water interface; if the focus is on benthic communities, then the appropriate substrate is the sediment-water interface. If the habitat contains both sediment-water and water-air interfaces, as is found in many riverine, lacustrine, and littoral communities, the sediment-water interface should be used so that atmobiotic individuals can be coded as living above both the primary substrate and their immediate, fluidic substrate (see Table 2).

Individuals with significant portions of their bodies simultaneously within and above substrates should be classified in both character states. Typical examples include aquatic pleuston that float partially submerged at the water's surface, benthic, semi-infaunal individuals that are only partially submerged in sediment, and trees that have extensive root structures. Note, however, that not all rooted individuals must be classified by both character states. While such a correlation is likely for trees, this relationship reflects more the biomechanical constraints of large, rooted individuals in terrestrial habitats than the ecological necessity of being rooted and having a significant portion of one's body in that rooting structure. A good counterexample is kelp, although these are less nutritionally dependent on their holdfast than are terrestrial trees (Dayton 1985). Individuals that live essentially above sediment but that sink passively into it, such as concavo-convex brachiopods and some scallops, should be coded as above the sediment unless they actively occupy both positions, such as some pectinid bivalves.

Note that this character is an *absolute* one, referring to the orientation of an individual in relation to the primary substrate of the entire habitat. The next character—immediate microhabitat—refers to the location of the individual from its own perspective. Individuals that live cryptically within the cavities of coral reefs or endoparasitically within another individual may be both above substrates in a primary sense (e.g., inhabiting a microhabitat situated above the sediment-water interface), but within substrates in an immediate sense (e.g., inhabiting a crevice or tissue). This character is further elaborated with continuous character 52 (primary stratification) below.

24. *Above primary substrate*—The individual lives above the primary substrate of the focal habitat. This character state includes superterranean, epibenthic, and epineustonic (i.e., living on the surface of water) individuals.
25. *Within primary substrate*—The individual lives within or below the primary substrate of the focal habitat. This character state includes subterranean and endobenthic individuals.

Immediate microhabitat—Typical resting location of an individual *relative* to its immediate substrate, whether geotropically oriented or not. Some individuals can simultaneously occupy both character states. The distinction with primary microhabitat is important, because many individuals, such as burrowing animals, live permanently within the substrate but also move freely within their burrow; such animals, therefore, would live above their immediate substrate, the burrow wall. Infaunal individuals that ''swim'' through substrates without creating a permanent burrow should be coded as living within their substrates. In contrast, planktonic, flying, and swimming individuals whose surrounding medium is fluid should be coded by the presence of both character states unless they only remain within a single stratum, in which case they should be coded as ''within'' their stratum. See further discussion under previous characters; this character is further elaborated with continuous character 53 (immediate stratification) below.

26. *Above immediate substrate*—The individual lives above its immediate substrate. This character state includes many epibiotic, ectoparasitic, and encrusting individuals.
27. *Within immediate substrate*—The individual lives within or below its immediate substrate. This character state includes subterranean, endobenthic, and endoparasitic individuals.

Support—Whether an individual supports itself or must rely on another structure (individual or material) to inhabit its primary microhabitat.

28. *Supported*—The individual relies on another structure to inhabit its primary microhabitat. Common examples include lianas (Givnish and Vermeij 1976; Putz 1984; Schnitzer and Bongers 2002), barnacles (Seilacher 2005), and other epibionts (Peters and Bork 1998) that use forms of attachment to maintain a different stratification state (characters 52–53) than they could otherwise, as well as infaunal burrow-dwellers that are unable to excavate burrows themselves. This excludes benthic individuals that attach to shells or other hard substrates as a source of attachment, but that do not gain a significant change in stratification. In this manner, it is independent of substrate relationship (character

states 22, 23 above). It can include free-living, mobile individuals if they position themselves atop structures to take advantage of particular stratification states. For example, many comatulid crinoids relocate atop reef crests during feeding (Meyer 1973); because their position depends on the reef framework, they are supported.

29. *Self-supported*—The individual inhabits its primary microhabitat without relying on other structures. This includes attached individuals that do not change their stratification state because of their attachment, as well as many free-living individuals. It includes mobile individuals, such as benthic gastropods and isopods, that roam over topographic features (and therefore stratigraphic states), except when the choice of substrate is conditional on a particular stratigraphic state that they could otherwise not attain themselves.

Primary feeding microhabitat—The location of an individual's food or where such food is acquired. Many individuals do not obtain food resources in the same location as their domicile. This segregation can be accomplished behaviorally by foraging (e.g., sea otters) or agriculture (e.g., leaf-cutter ants), or constructionally by manipulating feeding currents (e.g., serpulid polychaetes) or by setting traps (e.g., web-building spiders). As before, it is possible that some individuals can simultaneously derive food resources from both character states.

This character is an *absolute* one, referring to the orientation of an individual's food in relation to the primary substrate of the entire habitat. The next character refers to the location of the food from the individual's perspective. Thus, the food of leaf-mining insects may be above substrates in a primary sense, but also within substrates in an immediate sense. This character is further elaborated with continuous character 54 (primary food stratification) below.

30. *Above primary substrate*—The individual's food is above the primary substrate of the focal habitat.
31. *Within primary substrate*—The individual's food is within or below the primary substrate of the focal habitat.

Immediate feeding microhabitat—The location of an individual's food *relative* to its immediate substrate as the individual is foraging, whether geotropically oriented or not. Unlike the immediate feeding stratification, this coding is made with respect to the immediate substrate (or medium). Some individuals can feed in both character states. Flying and swimming individuals that forage in a fluid should be coded by the immediate position of its food. For example, the epibenthic food of a carnivorous fish that forages while swimming would be classified as below (or within) its foraging level. See further discussion under previous character; this character is further elaborated with continuous character 55 (immediate food stratification) below.

32. *Above immediate substrate*—The individual's food resource is located above its immediate substrate.
33. *Within immediate substrate*—The individual's food resource is located within or below its immediate substrate

Diet—The major dietary composition (largely carbohydrates) of an adult individual, regardless of the size of the food item. Character states are defined by the nutritional value of the diet, which generally parallels the cellular, metabolic, and organ-level diversity of taxonomic kingdoms. It is possible to subdivide this character to include more specific dietary types, including other taxonomic groups (algae, angiosperms, molluscs, fish, or culicids) or anatomical divisions (nuts, leaves, fruit, scales, or muscle). However, such divisions are not practical when comparisons are made across disparate habitats and large time scales.

Because most individuals are opportunistic to some degree, more than one character state often applies to the same individual; however, emphasis is on the primary dietary food items. An omnivore might be classified as eating both plant and animal matter, whereas many carnivorous plants would be listed only as autotrophic, because insects primarily supplement nitrogen (Ellison and Gotelli 2001). Individuals that acquire a majority of their dietary needs from dissolved organic molecules or from decomposing other individuals could potentially be included in any of the heterotrophic character states depending on the organic source. Individuals with obligate photosymbionts—lichen (Lutzoni et al. 2001), zooxanthellate corals (Rowan 1998), and many others (Rowan and Powers 1991)—should be coded as microbivores (typically incorporeal and ambient feeding; see below) because a major source of their carbohydrates is derived from their cyanobacterial or dinoflagellate photobionts; these individuals should be coded simultaneously in other states if they have other diets (such as microcarnivorous, hermatypic corals). Only those individuals that are truly autotrophic and heterotrophic, such as phytomastigophoran protists, can be simultaneously both autotrophic and heterotrophic.

The common term *detritivore* has been redefined here as *microbivore,* referring solely to the dietary composition of detritus, which is dominantly bacterial and protistan in marine settings (Plante et al. 1990); plant and fungal matter may also dominate in terrestrial ones, but such diets should be described as herbivorous and fungivorous, respectively. This character state refers neither to the deposited location of the food (e.g., as in ''deposit feeding''), nor to the particulate, fragmented condition of this food (e.g., as in particle feeding, see below).

34. *Autotroph*—Autotrophic individuals, whether photoautotrophic or chemoautotrophic, that assimilate carbon dioxide into complex biochemicals. This character state does not include heterotrophic individuals with obligate photosynthetic endosymbionts (see previous discussion of dietary character).
35. *Microbivore*—Heterotrophic individuals that acquire the majority of their nutrition from bacteria and protists, whether corporeal or admixed with disintegrated, decomposed, detrital, or particulate matter, and regardless of whether the food is resting, deposited, or suspended in the environment. Food in this character state includes unicellular microbes as well as colonial protists, bacterial films, slime molds, and coenocytic, filamentous, and macrophytic algae (Sieburth 1976). In marine settings, yeasts and meiofaunal animals, including nematodes and turbellarians, are often eaten with these microbes but are not typically a foraged food item (Fenchel 1978; Barnes and Hughes 1988). This character state does not include those terrestrial detritus feeders whose diet consists primarily of fungal or plant material. In general, note that this character state, when referring to individuals that eat detritus, is restricted to the microbially rich nutritional composition of detritus and not the physical condition of that food (see next character).

    The term microbivore is preferred over detritivore as a dietary character state because most detritus contains essentially no nutritive content aside from its affiliated microbial biota, and because many suspension feeders share the same diet as detritus feeders (Hunt 1925; Plante et al. 1990). Also included in this character state are fungi, protists, and bacteria that feed on other microorganisms, as well as organisms with endosymbiotic microbes (Plante et al. 1990). This character state could be subdivided into bacteriovore (or bacteriophage) and protistivore character states when such information is available.
36. *Carnivore*—Heterotrophic individuals (including fungi) that eat organic matter of animal origin, regardless of whether the food resource is alive or dead when acquired and ingested.
37. *Herbivore*—Heterotrophic individuals (including fungi) that

eat organic matter of plant origin, regardless of whether the food resource is alive or dead when acquired and ingested.

38. *Fungivore*—Heterotrophic individuals (including fungi) that eat organic matter of fungal origin, including yeasts, regardless of whether the food resource is alive or dead when acquired and ingested.

Physical condition of food—The physical condition of nutritional material acquired by an individual, regardless of the size of the food. Like many characters here, there is a strong element of scale-dependence (Hutchinson 1965). What may appear to be a particle feeder from our anthropomorphic perspective, such as a small, infaunal gastropod, may actually be a bulk feeder of nematodes and diatom films; amoeboids feeding on the same diatoms may also be bulk feeders. These character states are logically independent of the diet and foraging habit of the individual, although there may be a high correlation. These states are essentially identical to those described by Schmidt-Nielsen (1997), although he treats dissolved organics and sulfur-reducing bacteria as additional states.

39. *Incorporeal feeder*—Individuals that are able to self-sufficiently utilize ambient or dissolved radiant or inorganic chemical energy, without acquiring nutrients directly from other organisms. Lichens and other individuals with obligate photosymbionts that rely primarily on their photosymbionts for nutritional needs are included in this character state. Also included is the bivalve *Solemya* (Reid and Bernard 1980; Powell and Somero 1986), some olenomorph trilobites (Fortey 2000), and several epidermal-feeding crinoids (e.g., Silurian *Pygmaeocrinus*, *Paracolocrinus*, and microcrinoids [Brett 1984]) that lack or have significantly reduced mouthparts and digestive systems, that utilize sulfur-reducing bacterial symbionts, or that acquire a majority of their nutrition from dissolved organic matter.
40. *Solution feeder*—Individuals that acquire most of their nutritional requirements via dissolved nutrients, typically via diffusion or sucking, and without regard to the origin of the dissolved organic matter. Examples include decomposing fungi, saprophytic plants, many parasites and insects, vampire bats, lepidopterans, and hummingbirds. If individual life stages are included, nearly every juvenile mammal will be included in this state (Schmidt-Nielsen 1997). Fungi, arachnids, some insects, and other individuals with extracorporeal digestion are not included if they are in direct contact with their food source.
41. *Particle feeder*—Individuals that acquire most of their nutritional requirements via degraded, decomposed, or particulate organic matter. Note that this term is new and not to be confused with detritivory, microbivory, or deposit feeding. Particle feeding refers strictly to the particulate condition of the food; detritivory (and its form used here, microbivory) refers to dietary composition; and deposit feeding refers to the physical location of that food, sometimes also referring to the foraging behavior used to feed on such material (as its form used here, mass feeding) (Plante et al. 1990). In fact, many suspension feeders and deposit feeders eat the same particulate food items, differing solely in their foraging habits (Hunt 1925; Plante et al. 1990). Microorganisms—intact bacteria, protists, and fungi—are included here as particulate organic matter when they are freely distributed in a foraged environment.
42. *Bulk feeder*—Individuals that obtain most of their nutritional requirements via nutrients stored in portions of, or entire bodies of, macroscopic organisms *en bloc*, whether animal, plant, fungal, protistan, or algal (i.e., macrophytic algae), alive or dead, but which have not undergone significant decomposition or fragmentation. This character state can include a variety of foraging habits, including many predators, grazers, burrowers, and suspension feeders. Metazoan microbivores may be included here when the microorganismal flora constitutes mats, films, molds, syncytia, or other aggregated masses that require food-handling abilities to be eaten. If the focal habitat is not macroscopic, then individual microorganisms may be considered as bulk food.

Feeding habit—The means by which food is acquired, whether via direct manipulation, physical contact, or indirect acquisition. For mobile animals, this is synonymous with foraging behavior. This character also includes all individuals that acquire nutrition without active movement, although some degree of adaptation, whether genetic or ecophenotypic, is generally involved. Feeding habits generally involve the processes of food detection, incapacitation, and manipulation. Thus, these behaviors are complex and generally require numerous coordinated structures and behaviors. Although this character is not subdivided into discrete subcharacters related to each of these processes, it is intended that the following character states accurately characterize the primary methods in which individuals acquire food.

43. *Ambient feeder*—Individuals that acquire nutrients across body walls without active attachment to or manipulation of a food source. Although plants and some other sedentary individuals do not actively detect food, competition still causes mortality of saplings, seeds, or other juveniles that are not capable of meeting basic nutritional requirements. Optimization of energy intake can still take place in sedentary autotrophs via growth and movement of leaves, stalks, zooxanthellate carrier cells, cellular pigmentation, and other energy-harvesting structures. This character state also includes numerous endoparasites and other individuals that acquire nutrients or dissolved organic molecules via diffusion across a body wall, but without active attachment to their host.
44. *Filter feeder*—Individuals that acquire nutrients, regardless of dietary composition and condition, suspended in some fluid through the use of sieves and nets, fibers, setules, mucous traps, pores, or other filters (Rubenstein and Koehl 1977). These individuals may use a variety of active means by which to capture, entrain, or direct nutrient-laden feeding currents by these structures, although passive suspension feeders are also included by this definition (LaBarbera 1984). Included are diverse individuals: carnivores—including corals; microbivores—including sea pens and brittlestars; more renowned filter feeders—from crinoids to bivalves; and less renowned ones as well—including arachnids and mysticete whales. Some traditional deposit feeders are also included here, including some polychaetes and aquatic insect larvae (Vogel 1994). Note that not all suspension feeders use a filter to capture nutrients (see raptorial feeding below).
45. *Attachment feeder*—Individuals that acquire nutrients, regardless of dietary composition and condition, by actively and directly attaching to the food source, regardless of the duration of attachment. The prey or food item is typically larger than the feeding individual, although this is not necessary. Examples include ectoparasitic insects and arachnids, coprophagous platyceratid gastropods that position themselves above the anus of crinoids (Keyes 1888; but see Gahn and Baumiller 2003), agnathan fish, saprophytes, and some fungi.
46. *Mass feeder*—Individuals that acquire nutrients, regardless of dietary composition and condition, by capturing edible, and sometimes inedible or not eaten, material en masse. In all cases, the primary criterion is that multiple food items are processed simultaneously, through ingestion, systematic harvesting, or food manipulation. The prey or food item is sometimes larger than the feeding individual, such as leaf-mining insects and some fungi and parasites. Individuals are often adapted for continuous feeding or temporary

TABLE A1. Ordered scale for skeletal body volume.

State	Volume (ml)	Code
Hectolitric	≥100, 000	9
Decalitric	10,000–100,000	8
Litric	1,000–10,000	7
Decilitric	100–1000	6
Centilitric	10–100	5
Millilitric	1–10	4
Submillilitric	0.1–1	3
Supramicrolitric	0.01–0.1	2
Microlitric	0.001–0.01	1
Submicrolitric	<0.001	0

storage of food items. Individuals that ingest or churn up substrates to extract food, and some browsers and grazers that ingest mass quantities of herbage, are also included here. Individuals feeding on carrion or other necrolyzed, fragmented, or decomposed matter, or on food living within such matter, may be included here when active raptorial methods are not evident, such as occurs in jawless amphinomid polychaetes (Fauchald and Jumars 1979). Examples of typical mass feeders include earthworms, nuculoid bivalves, artiodactyl mammals, and many polychaetes, holothurians, and some trilobites. A less obvious example includes rodents that gather food within cheek pouches and store it in caches or middens. Because this state is independent of selectivity (see next character), it is understandable that sediment ingestion or food gathering often is followed by selective storage, regurgitation, or mass defecation of inedible material if the ingestion is not selective.

47. *Raptorial feeder*—Individuals that acquire nutrients, regardless of dietary composition and condition, by actively seizing and manipulating individual food items. Unlike the previous state, the primary criterion is that feeding is concentrated on individual food items; thus, specialized detection, incapacitation, and manipulation structures and behaviors are required. This character state includes most predators (motile stalkers, ambush predators, and sessile opportunists) as well as some grazing and browsing herbivores, microbivores, and scavengers that have specialized means of selecting and acquiring food items. It also includes those suspension-feeding animals—such as scan-and-trap copepods and tentacular corals (Koehl 1981; Koehl and Strickler 1981; LaBarbera 1984)—that seize individuals without the use of a filtration device. Although most individuals in this character select their prey prior to seizing it (see feeding selectivity next), this is not necessary. A less selective example is the sawfish, which, in part, chaotically thrashes its toothy saw into a school of fish to wound its prey before eating (Breder 1952; Bigelow and Schroeder 1953; McEachran and de Carvalho 2002).

(Feeding selectivity)—The degree to which food resources are selected for consumption.

48. *Non-selective*—Food resources are not sorted during consumption, often with mass excretion of inedible material.
49. *Selective*—Food resources are sorted from non-food items prior to consumption, whether through direct selection, mechanical sorting, or immediately prior to ingestion, such as occurs in the production of bivalve pseudofeces. This character state also applies in the case of autotrophic individuals that have the ability to sort usable from unusable energy through the use of photoreceptive pigmentation or other means.

TABLE A2. Ordered scale for stratification. The same scale is used for primary and immediate stratification, as well as for the stratifications of food source.

Distance (cm)	Code
≥100.0	4
10.0–100.0	3
1.0–10.0	2
0.1–1.0	1
<0.1	0

50. *Secondarily selective*—Food resources are sorted after consumption, typically involving mass consumption of food and non-food items followed by regurgitation of inedible material.

Ordered, multistate characters.—These characters are coded according to the scales noted below.

51. **Skeletal body volume**—The body volume of the skeleton (or easily fossilized hard parts) of adult, sexually mature individuals. It would be preferable to use the more meaningful character of body mass; however, such a measure is not possible with most fossil taxa (but see Powell and Stanton 1985). While body volume is intended as a proxy for body mass and the relative energy utilization of a fossil individual, it is more accurately used here as a measure of spatial allocation. This altered meaning still incorporates scaling information relevant to mobility, defense from predators, diet selection, and the manner in which individuals negotiate their environment (see Novack-Gottshall in press). Body volume includes the space enclosed by the skeleton that may or may not include living tissue. The scale (Table A1) and allometric equation (A1) are based on empirical observations on the body volume of taxonomically and morphologically diverse taxa inhabiting deep-subtidal, soft-substrate habitats during the Cambrian through Devonian (Novack-Gottshall in press).

$$\text{Volume} = 0.544(\text{ATD})^{0.896} \quad \text{(A1)}$$

where ATD is the product of the three major body axes (the anterioposterior, transverse, and dorsoventral axes) measured in units centimeter. This equation may not be appropriate for other taxa, or for those outside the range 0.01–1000 ml. For further discussion, including estimation of confidence intervals and standard error, see Novack-Gottshall (in press).

52. **Primary stratification**—The typical maximum distance (Table A2) that an individual inhabits away from the primary substrate of the focal habitat, regardless of whether the individual lives above or within the substrate. This character supplements primary microhabitat (character states 24, 25); refer there for further details. In many ecological studies, primary stratification is also known as the stratum or tiering layer (Elton and Miller 1954; Turpaeva 1957; Ausich and Bottjer 1982; Bottjer and Ausich 1986). Because this character does not distinguish between individuals that live above and within substrates, it refers equally to stratification of forests (i.e., ground story, understory/midstory, and high canopy), epibenthos (i.e., reclining, elevated, and highly elevated), and endobenthos (shallow and deep infaunal) if coding with respect to the sediment-water or sediment-air interfaces.

Note that this character refers to the primary metabolic mass of a typical, sexually mature (if applicable) adult individual and not to any supportive, reproductive, protru-

TABLE A3. Ordered scale for spatial patterning.

Spatial patterning	Mean/variance	Code
Uniform	$\gg$1.0	2
Random	~1.0	1
Aggregated (gregarious)	$\ll$1.0	0

TABLE A4. Ordered scale for relative metabolic rate.

Relative metabolic rate	MSMI (L $O_2h^{-1}kg^{-1}$)	Code
Energetic	$\gg$1.0	2
Moderate	~1.0	1
Inactive	$\ll$1.0	0

sive, or attaching organs or appendages; typical examples of such masses include tree canopies, crinoid calyces, tetrapod trunks, and fungal vegetative mycelia. In many cases, this distance will correspond to one of the principal body size axes, but this is not necessary.

Note that this character is an *absolute* one, referring to the maximum height of an individual from the primary substrate of the entire habitat. The next character refers to the height of the individual relative to its immediate substrate. Thus, birds and bromeliads that live habitually within the high forest canopy may be both highly elevated in a primary sense (i.e., more than 10 m above the forest floor), but reclining in an immediate sense (i.e., inhabiting the surface or crevices of branches). See further discussion for immediate stratification (character 53) and Table 2 (in text).

The scale (Table A2) was selected from empirical observations on the stratification of taxa inhabiting deep-subtidal, soft-substrate habitats during the Cambrian through Devonian. The same scale is used for characters 53–55. Extrapolations or modifications can be made in future studies depending on their requirements.

53. **Immediate stratification**—The typical maximum distance (Table A2) that an individual generally inhabits away from its immediate substrate, regardless of whether the individual lives above or within the substrate. This value typically corresponds to the diameter of individuals that live within their immediate substrate. Unlike the previous character that is typically measured as a vertical distance, this distance can assume any orientation. This character supplements immediate microhabitat (character states 26, 27); refer there for further details. Corals that build robust frameworks should be coded only by the thickness of the living polyp layer; they are stratified in a primary sense (character 52) by the thickness of the entire multi-generational, skeletal framework. The coding scheme (Table A2) is the same as for character 52 (primary stratification).

54. **Primary food stratification**—The typical maximum distance of an individual's primary food resources from the primary substrate of the focal habitat, regardless of whether the individual lives above or within the substrate. When food is found in multiple microhabitats, this character refers to the maximum distance at which any dominant food item is found. Although many food items in a habitat are allochthonous in origin (e.g., particulate organic matter and some carrion), this character is concerned only with the location of food where it is utilized by the individual and not with its origin. For autotrophic (i.e., chemosynthetic and photosynthetic) individuals, this character records the location where energy oxidation occurs and not the location of the sun (i.e., photoautotrophic) or the earth's interior (i.e., deep-sea chemoautotrophs). This character supplements primary feeding microhabitat (character states 30, 31); refer there for further details. The coding scheme (Table A2) is the same as for character 52 (primary stratification).

55. **Immediate food stratification**—The typical maximum distance of an individual's typical food source away from itself, regardless of whether the individual lives above or within the substrate. Note that this is measured not from a substrate but from the food handling portion of the individual. For individuals that move while foraging, this character is the typical search distance involved in finding its food. For example, a mass-feeding polychaete that swallows food-bearing sediment would be coded as 0 if it feeds in place, whereas a hawk that searches for prey from the sky could be coded as 4 or greater. This character supplements immediate feeding microhabitat (character states 32, 33); refer there for further details. The coding scheme (Table A2) is the same as for character 52 (primary stratification).

56. **(Mobile velocity)**—The typical maximum speed used in moving, or a measure of energy expended in the act of mobility. This character could be subdivided to reflect either self-propelled velocity or the actual velocity of the individual regardless of energy expended (as in the case of epibiotic or planktonic individuals). This character is not feasible currently with most fossil individuals, and so an appropriate scale is not proposed.

57. **(Spatial patterning)**—Description of the spatial patterning of populations of individuals. Different populations of the same species can display different degrees of spatial patterning, but a single pattern should be found for each species in a single sample. Following convention (Hayek and Buzas 1997) (Table A3), spatial patterning is defined by the ratio of the mean density of individuals within samples to the variance of that estimate. More powerful statistical methods might be preferable (Hurlbert 1990). Common examples of gregarious individuals include Silurian *Pentamerus* brachiopod assemblages (Ziegler et al. 1966), ophiuroid assemblages, bryophyte mats, and birch assemblages. A uniform distribution can imply a negative interaction among individuals (Hayek and Buzas 1997).

58. **(Dispersal distance)**—The typical dispersal distance of an individual. Although this may correspond to geographic range for many planktotrophic marine species (Jablonski and Lutz 1983; Jablonski 1986; Brown 1995), this is not always the case for terrestrial species (Howe and Smallwood 1982; Sutherland et al. 2000). This character is not feasible currently with most fossil populations, and so an appropriate scale is not proposed.

59. **(Relative metabolic rate)**—The absolute metabolic rate (or rate of oxygen consumption) of an individual often scales with body mass to the power of 0.75 (Schmidt-Nielsen 1997). When such observations are available, the mass-specific metabolic index (MSMI) can be calculated:

$$\text{MSMI} = \text{metabolic rate}/(\text{body size})^{0.75}. \qquad \text{(A2)}$$

When such estimates are not available, the following approximate coding (Table A4) can be used. In many cases, an approximate metabolic rate of extinct taxa can be estimated from living relatives (Powell and Stanton 1985; Bambach 1999; Bambach et al. 2002).

60. **(Life span)**—The typical life span of an individual. This character is not available readily with most fossils, and so an appropriate scale is not proposed.

Appendix B

Demonstration of Coding for Extinct and Extant Species

The following two examples—one extant and one extinct—demonstrate how species can be coded with the ecospace framework. In both instances, only 44 characters and states from the larger ecospace framework were used for which reliable information was available for living and fossil biotas (Table 3). All other taxa in the Paleozoic and modern databases were coded using similar criteria.

The living, inarticulated brachiopod *Glottidia pyramidata* (Stimpson) (Family Lingulidae) belongs to one of the oldest living families (West 1976; Kowalewski et al. 1997). *G. pyramidata* is sexual and gonochoristic (Williams et al. 2000; Paine 1963). As an adult, *G. pyramidata* lives within the sediment (its primary microhabitat) at a typical depth of 0 to 5 cm in a U-shaped burrow with the anterior commissure at the sediment surface (Paine 1963; Thayer and Steele- Petrović 1975). This burrow is not typically cohesive, and so the brachiopod lives within its immediate, unconsolidated substrate. It is able to move by means of a muscular pedicle when disturbed—either withdrawing into its burrow or physically changing locations—but it remains sedentary typically, with the pedicle impermanently attached to sediment; thus, it is facultatively mobile, self supporting, and attached. Suspended food particles (primarily phytoplankton, although animal larvae, sand, and detritus are sometimes found [Paine 1963]) are brought from the overlying water with the lophophore; it is a particle-feeding microbivore that acquires food with a filter (in the broad sense, cf. Vogel 1994). A typical specimen has an estimated skeletal body volume of approximately 0.714 ml (using measurements from Williams et al. 2000 and equation A1).

Isotelus maximus (Family Asaphidae) was a massive trilobite found throughout present-day eastern North America during the Late Ordovician (Harrington et al. 1959). From the buttressed hypostome with posterior notch, Fortey and Owens (1999) inferred that it had a predatory habit and that the hypostome likely was used to manipulate prey. This predatory conclusion is supported further by trace fossils, with *Rusophycus* corresponding to the genus superimposed on a *Palaeophycus* worm burrow (Brandt et al. 1995; Fortey and Owens 1999). These *Rusophycus* do not demonstrate a churning behavior, instead showing raptorial attacks with evidence of large appendages. The absence of other attributable trace fossils—for an otherwise distinctive trilobite—argues that this was a generally epibenthic, free-living, habitually mobile animal that did not burrow into sediment except surficially when feeding. It is unclear how high in the water column it swam, but it was likely primarily benthic, judging from its large size and flattened profile. It perhaps fed on benthic prey items at or above the sediment-water interface; the large, raised eyes are evidence that it could locate prey from a distance. There are no known asexual trilobites, and it was likely gonochoristic. A typical specimen of the species has an approximate skeletal body volume of 269 ml (using measurements from Feldman 1996 and equation A1).

Literature Cited in Appendices

Ausich, W. I., and D. J. Bottjer. 1982. Tiering in suspension feeding communities on soft substrata throughout the Phanerozoic. Science 216:173–174.

Bambach, R. K. 1999. Energetics in the global marine fauna: a connection between terrestrial diversification and change in the marine biosphere. Geobios 32:131–144.

Bambach, R. K., A. H. Knoll, and J. J. Sepkoski Jr. 2002. Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm. Proceedings of the National Academy of Sciences USA 99:6854–6859.

Barnes, R. S. K., and R. N. Hughes. 1988. An introduction to marine ecology, 2d ed. Blackwell Scientific, Boston.

Bassett, M. G. 1984. Life strategies of Silurian brachiopods. *In* M. G. Bassett and J. D. Lawson, eds. Autecology of Silurian organisms. Special Papers in Palaeontology 32:237–264.

Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Western North Atlantic, No. 1, Part 2. Sawfishes, guitarfishes, skates, and rays; chimaeroids. Memoirs of the Sears Memorial Foundation for Marine Research 1:1–514.

Bottjer, D. J., and W. I. Ausich. 1986. Phanerozoic development of tiering in soft substrata suspension-feeding communities. Paleobiology 12:400–420.

Brandt, D. S., D. L. Meyer, and P. B. Lask. 1995. *Isotelus* (Trilobita) ''hunting burrow'' from Upper Ordovician strata, Ohio. Journal of Paleontology 69:1079–1083.

Breder, C. M., Jr. 1952. On the utility of the saw of the sawfish. Copeia 1952:90–91.

Brett, C. E. 1984. Autecology of Silurian pelmatozoan echinoderms. *In* M. G. Bassett and J. D. Lawson, eds. Autecology of Silurian organisms. Special Papers in Palaeontology 32:87–120.

Brusca, R. C., and G. J. Brusca. 2002. Invertebrates, 2d ed. Sinauer, Sunderland, Mass.

Campbell, N. A., and J. Reece. 2005. Biology, 7th ed. Benjamin Cummings, New York.

Dayton, D. K. 1985. The ecology of kelp communities. Annual Review of Ecology and Systematics 16:215–245.

Ellison, A. M., and N. J. Gotelli. 2001. Evolutionary ecology of carnivorous plants. Trends in Ecology and Evolution 16:623–629.

Elton, C. S., and R. S. Miller. 1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. Journal of Ecology 42:460–496.

Fauchald, K., and P. A. Jumars. 1979. The diet of worms: a study of polychaetes feeding guilds. Oceanography and Marine Biology Annual Review 17:193–284.

Feldmann, R. M., ed. 1996. Fossils of Ohio. Ohio Division of Geological Survey Bulletin 70.

Fenchel, T. M. 1978. The ecology of micro- and meiobenthos. Annual Review of Ecology and Systematics 9:99–121.

Fortey, R. A. 2000. Olenid trilobites: the oldest known chemoautotrophic symbionts? Proceedings of the National Academy of Sciences USA 97:6574–6578.

Fortey, R. A., and N. C. Hughes. 1998. Brood pouches in trilobites. Journal of Paleontology 72:639–649.

Fortey, R. A., and R. M. Owens. 1999. Feeding habits in trilobites. Palaeontology 42:429–465.

Gahn, F. J., and T. K. Baumiller. 2003. Infestation of Middle Devonian (Givetian) camerate crinoids by platyceratid gastropods and its implications for the nature of their biotic interaction. Lethaia 36:71–82.

Givnish, T. J., and G. E. Vermeij. 1976. Sizes and shapes of liane leaves. American Naturalist 110:743–778.

Harrington, H. J., G. Henningsmoen, B. F. Howell, V. Jaanusson, C. Lochman-Balk, R. C. Moore, C. Poulsen, F. Rasetti, E. Richter, R. Richter, H. Schmidt, K. Sdzuy, W. Struve, L. Størmer, C. J. Stubblefield, R. Tripp, J. M. Weller, and H. B. Whittington. 1959. Arthropoda 1, Trilobitomorpha. Part O of R. C. Moore, ed. Treatise on invertebrate paleontology. Geological Society of America, New York, and University of Kansas, Lawrence.

Hayek, L. C., and M. A. Buzas. 1997. Surveying natural populations. Columbia University Press, New York.

Horner, J. R. 2000. Dinosaur reproduction and parenting. Annual Review of Earth and Planetary Sciences 28:19–45.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201–228.

Hunt, O. D. 1925. The food of the bottom fauna of the Plymouth fishing grounds. Journal of the Marine Biological Association, UK 13:560–599.

Hurlbert, S. H. 1990. Spatial distribution of the montane unicorn. Oikos 58:257–271.

Hutchinson, G. E. 1965. The ecological theater and the evolutionary play. Yale University Press, New Haven, Conn.

Jablonski, D. 1986. Larval ecology and macroevolution in marine invertebrates. Bulletin of Marine Science 39:565–587.

Jablonski, D., and R. A. Lutz. 1983. Larval ecology of marine invertebrates: paleobiologic implications. Biological Reviews 58:21–89.

Keyes, C. R. 1888. The sedentary habits of *Platyceras*. American Journal of Science 36:269–272.

Koehl, M. A. 1981. Feeding at low Reynolds number by copepods. Lectures on Mathematics in the Life Sciences 14:89–117.

Koehl, M. A., and J. R. Strickler. 1981. Copepod feeding currents: food capture at low Reynolds number. Limnology and Oceanography 26:1062–1073.

Kowalewski, M., E. Dyreson, J. D. Marcot, J. A. Vargas, K. W. Flessa, and D. P. Hallman. 1997. Phenetic discrimination of biometric simpletons: paleobiological implications of morphospecies in the lingulide brachiopod *Glottidia*. Paleobiology 23:444–469.

LaBarbera, M. 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. American Zoologist 24:71–84.

Lincoln, R. J., G. A. Boxshall, and P. F. Clark. 1992. A dictionary of ecology, evolution, and systematics. Cambridge University Press, New York.

Lutzoni, F., M. Pagel, and V. Reeb. 2001. Major fungal lineages are derived from lichen symbiotic ancestors. Nature 411:937–940.

McEachran, J. D., and M. R. de Carvalho. 2002. Pristidae. Sawfishes. Pp. 524–526 *in* K. E. Carpenter, ed. FAO species identification guide for fishery purpose: the living marine resources of the western central Atlantic, Vol. 1. Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes, and chimaera. FAO, Rome.

Meyer, D. L. 1973. Feeding behavior and ecology of shallow-water unstalked crinoids (Echinodermata) in the Caribbean Sea. Marine Biology 22:105–129.

Novack-Gottshall, P. M. In press. Using simple body size metrics to estimate fossil body volume: empirical validation using diverse Paleozoic invertebrates. Palaois 23.

Paine, R. T. 1963. Ecology of the brachiopod *Glottidia pyramidata*. Ecological Monographs 33:187–213.

Peters, S. E., and K. B. Bork. 1998. Secondary tiering on crinoids from the Waldron Shale (Silurian: Wenlockian) of Indiana. Journal of Paleontology 72:887–894.

Plante, C. J., P. A. Jumars, and J. A. Baross. 1990. Digestive associations between marine detritivores and bacteria. Annual Review of Ecology and Systematics 21:93–127.

Powell, E. N., and R. J. Stanton Jr. 1985. Estimating biomass and energy flow of molluscs in palaeo-communities. Palaeontology 28:1–34.

Powell, M. A., and G. N. Somero. 1986. Hydrogen sulfide oxidation is coupled to oxidative phosphorylation in mitochondria of *Solemya reidi*. Science 233:563–566.

Putz, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65:1713–1724.

Raven, P. H., R. F. Evert, and S. E. Eichhorn. 2004. Biology of plants. W. H. Freeman, San Francisco.

Reid, R. G. B., and F. R. Bernard. 1980. Gutless bivalves. Science 208:609–610.

Richardson, J. R. 1981. Brachiopods and pedicles. Paleobiology 7:87–95.

Richardson, J. R., and J. E. Watson. 1975a. Form and function in a Recent free living brachiopod Magadina cumingi. Paleobiology 1:379–387.

———. 1975b. Locomotory adaptations in a free-lying brachiopod. Science 189:381–382.

Rowan, R. 1998. Diversity and ecology of zooxanthellae on coral reefs. Journal of Phycology 34:407–417.

Rowan, R., and D. Powers. 1991. A molecular genetic classification of zooxanthellae and the evolution of animal-algal symbioses. Science 251:1348–1351.

Rubenstein, D. I., and M. A. Koehl. 1977. The mechanisms of filter feeding: some theoretical considerations. American Naturalist 111:981–994

Schmidt-Nielsen, K. 1997. Animal physiology: adaptation and environment, 5th ed. Cambridge University Press, New York.

Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests. Trends in Ecology and Evolution 117:223–230.

Seilacher, A. 2005. Whale barnacles: exaptational access to a forbidden paradise. *In* E. S. Vrba and N. Eldredge, eds. Macroevolution: diversity, disparity, contingency. Paleobiology 31(Suppl. to No. 2):27–35.

Sieburth, J. M. 1976. Bacterial substrates and productivity in marine ecosystems. Annual Review of Ecology and Systematics 7:259–285.

Stanley, S. M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). Geological Society of America Memoir 125.

Surlyk, F. 1972. Morphological adaptations and population structures of the Danish chalk brachiopods (Maastrichtian, Upper Cretaceous). Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter 19:1–57.

Sutherland, G. D., A. S. Harestad, K. Price, and K. P. Lertzman. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Conservation Ecology 4:16.

Taylor, P. D., and M. A. Wilson. 2002. A new terminology for marine organisms inhabiting hard substrates. Palaios 17:522–525.

Thayer, C. W., and H. M. Steele-Petrović. 1975. Burrowing of the lingulid brachiopod *Glottidia pyramidata*: its ecologic and paleoecologic significance. Lethaia 8:209–221.

Turpaeva, E. P. 1957. Food interrelationships of dominant species in marine benthic biocoenoses. Transactions of the Institute of Oceanology (Marine Biology) 20:137–148.

Vogel, S. 1994. Life in moving fluids, 2d ed. Princeton University Press, Princeton, N.J.

West, R. R. 1976. Comparison of seven lingulid communities. Pp. 171–192 *in* R. W. Scott and R. R. West, eds. Structure and classification of paleocommunities. Dowden, Hutchinson, and Ross, Stroudsburg, Penn.

Williams, A., C. H. C. Bruton, and S. J. Carlson. 2000. Brachiopoda (revised). Part H of R. C. Moore, ed. Treatise on invertebrate paleontology. Geological Society of America, New York, and University of Kansas, Lawrence.

Ziegler, A. M., A. J. Boucot, and R. P. Sheldon. 1966. Silurian pentameroid brachiopods preserved in position of growth. Journal of Paleontology 40:121–122.