Chapter 4

SYSTEMATICS

In the previous chapter, we discussed the nature and recognition of species. An important observation, predating the acceptance of biological evolution, is that all known species, despite their great numbers and enormous differences, appear to be naturally organized into more inclusive units. **Systematics,** broadly speaking, is the study of the diversity of organisms and the relationships among them. A major part of systematics is **taxonomy,** the theory and practice of describing and classifying organisms. Systematics accounts for a large part of all paleontological research, and the results of systematic studies form the foundation of many other areas of investigation. In this chapter, we focus on the procedures most important to practicing paleontologists: species description, inference of evolutionary relationships, and classification of species into more inclusive taxa or higher categories.

4.1 FORMAL NAMING AND DESCRIPTION OF SPECIES

A new species can be erected in biology or paleontology either because previously unnamed specimens have become available or because a previously recognized species is judged actually to be two or more species. An individual worker's views on the breadth of species and on the division of genera into species are guided by judgment that reflects the accumulated experience with a group of organisms (Chapter 3). In contrast, the formal naming of species is governed by widely accepted systems of rules and procedures. One of the most important of these systems is the *International Code of Zoological Nomenclature*. The Code applies to taxonomic categories from the subspecies to the superfamily. Emphasis in this chapter will be on its application to the species category.

A comparable set of procedures for plants is known as the *International Rules of Botanical Nomenclature*. In addition, other rules are commonly used for groups like the bacteria. Because these codes are independent, it is possible for the same formal name to be applied both to a plant and an animal, although in practice this is uncommon. For our purposes, the differences between these codes are minor. (For example, the Botanical Code requires a new species name to be accompanied by a description or diagnosis in Latin—a rule that, perhaps fortunately for the paleontologist, does not apply to fossils.) We will therefore focus on the Zoological Code. The possibility of adopting a single set of standard rules for plants and animals has been seriously discussed but not yet implemented.

For a species to be officially recognized, it must be given a name in binomial form; that is, the name must consist of two words. The official name for the human genus is *Homo*, and *Homo sapiens* is the species name. A species name like *sapiens* (sometimes called the *trivial name* or *epithet*) is meaningless unless associated with a genus name. In practice, most newly discovered species can be assigned readily to an existing genus and thus the act of describing a new species involves the invention of only one name. If the new species cannot be accommodated within an established genus, a new genus must be erected and named at the same time, and the new species is assigned to it.

Except for the genus assignment just mentioned, the Code does not insist on the complete classification of a new species at all levels from the family up to the kingdom, recognizing that complete classification is often difficult or impossible, particularly if the new species is quite distinct from all other known species.

Another requirement of the new name is that it not already be in use (**occupied**). This restriction refers to the combination of genus and species names. By convention, repeating trivial names in closely related genera is also avoided because genus affiliations may change as knowledge of the evolutionary relationships between species changes.

The names for species and genera must be Latin words or words that have been latinized. There is considerable latitude in the choice of words to be used as names—latinized place names, names of people, and descriptive words are all used.

For the name of a new species to be recognized, it must be published in an approved and widely accessible medium. A new name is not officially recognized if it has been used only in the labeling of a museum specimen or described orally before a scientific meeting. Nor is anonymous publication recognized. If a new species name is erected according to the rules of nomenclature and is validly published, it is said to be **available.** The nature of publication itself has evolved over the history of biological nomenclature, and the Code has changed to reflect this. Until recently, a new species name had to be published in ink on paper. The latest edition of the Code also recognizes publication in media such as read-only optical disks, although conventional print is still recommended. Dissemination over the Internet is not recognized, although this may soon change. To simplify bibliographic work, the Code recommends that publication be in French, German, English, or Russian.

The Code specifies that each newly described species be accompanied by the designation of a type specimen or set of type specimens. Type specimens must be clearly labeled, and suitable measures must be taken for their preservation and accessibility, which means that type specimens are usually deposited in a major museum where curatorial facilities are available. Illustration of specimens is strongly recommended and may be considered mandatory.

The type specimens do not in fact *define* a species; rather, they are the name bearers for that species. When a species is named, the name is formally attached only to the one or more specimens that are designated as type specimens. In practice, type specimens are often somewhat unusual representatives of the species (see Figure 3.19). The most common biases are toward large size and good preservation.

If a single specimen is designated, it is called the **holotype.** If several specimens serve this purpose, they are called **syntypes.** Both alternatives are officially acceptable, although the Code urges the use of a holotype rather than a series of syntypes because it is always possible that the series will be judged by later workers to contain representatives of more than one species.

Several other kinds of type specimens figure prominently in taxonomic work. A **paratype** is a specimen other than the holotype, which is formally designated by the author of a species as having been used in the description of the species. The designation of a single holotype and a series of paratypes thus contains some of the advantages of both the holotype system and the syntype system. The holotype remains the name bearer but the paratypes, which may be numerous, serve to express more fully the author's concept of the species. Some of the more important kinds of types are summarized in Table 4.1.

TABLE 4.1

Kinds of Type Specimens

Name	Usage	Etymology
Holotype	Single specimen designated as name bearer	*holo-*, complete
Syntypes	Several specimens designated as name bearers	*syn-*, together
Paratype	Specimen, other than holotype, used in species description	*para-*, side by side
Lectotype	Syntype later chosen as definitive type	*lecto-*, chosen
Neotype	Replacement for lost or destroyed type	*neo-*, new
Plesiotype	Specimen used in redescription of existing species	*plesio-*, near

A description of a new species typically contains a number of elements:

1. *Headings* include the name and author of the genus and other higher taxa to which the species is assigned.
2. The *scientific name* is in binomial form.
3. *Figure numbers* indicate where in the publication the species is illustrated.
4. The *diagnosis* is a listing of characteristics by which the new species can be distinguished from other species.
5. *Type material* is explicitly listed.
6. The *etymology* explains the derivation of the name.
7. A *description* is given; in this context, a description is a full assessment of characteristics without particular reference to similarities and differences relative to other recognized species.
8. A *discussion* section may include information about nongenetic variation, ontogenetic stages, evolutionary affinities with other species, and, for fossils, state of preservation.
9. A section on *occurrence* lists information on habitat and, for fossils, stratigraphic horizon.
10. The *distribution* section may be a list of places at which the new species has been found (in addition to the type locality). With regard to habitat, paleontologists are most concerned with the geologic setting (rock type, for example).

In addition to these standard parts of a description, it is also common to include a list of material examined, with reference to museum repositories of specimens other than those formally designated as types, and a section with biometric data. At a minimum, the major dimensions of the type specimen or specimens should be included. For a description of a new species based on previously known material, or for a redescription of a known species, the species description typically also includes a section on taxonomic references and a history of nomenclature for the species.

Three actual examples of species description are given in Boxes 4.1, 4.2, and 4.3, with illustrations of type specimens.

Because one of the prime objectives of diagnosis and description is communication of information, there is a premium attached to consistency. This means, for example, that standardized morphologic terminology is used wherever possible. The description, as distinct from the diagnosis, serves several purposes—not the least important of which is to provide an assessment of attributes that may at some future time be critical in diagnosis. If the species is part of a well-known group and is similar in most regards to other species, much of the description may be neglected in deference to the existing descriptions of closely related species, and a simple diagnosis may suffice.

For a species belonging to a relatively unknown group, the description must be more comprehensive so that relevant comparisons can be made if related species are discovered subsequently. When a new species is assigned to a new genus and family containing only that species, the diagnoses of the species, genus, and family will generally be quite similar. In such cases, the genus and family diagnoses are likely to require revision if closely related species are discovered in the future.

If possible, a description should include discussion of ontogenetic development, particularly if the organism's ontogeny is accompanied by a substantial change in form. Also important is an assessment of variation encountered within and between populations of the species.

How much specimen material is necessary to establish a new species? No unequivocal answers can be given to this question because what is necessary and possible in a particular description depends on the amount of difference between related species and on the quantity and quality of preserved material. Often a single specimen demonstrates that the organism is different from all other known organisms. On the other hand, if a new species belongs to a well-known group in which differences between species tend to be rather subtle, a large amount of material must be accumulated to make the description complete and effective and to establish that the new species is truly distinct from other, related species [SEE SECTION 3.2].

There are some noteworthy cases in which different parts of a fossil organism were initially described as separate species because they were found in isolation. Only later were the different "species" found in association in such a way that they clearly belong to the same organism [SEE SECTION 10.2]. The Upper Devonian **PROGYMNOSPERM** *Archaeopteris* represents a striking but by no means unique case. The leafy branches of *Archaeopteris* were first described in the 1870s, and the genus *Callixylon* was erected in 1911 for various woody stems. Although both genera are very common and were sometimes found in the same sedimentary

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Box 4.1

STENOSCISMA PYRAUSTOIDES COOPER AND GRANT, N. SP.

The following refers to Figure 4.1 and Table 4.2.

Large for genus; outline broadly subelliptical to subtrigonal, sides diverging between 80° and 125°, normally over 100° in adults, maximum width near midlength, normally slightly farther toward the anterior; profile strongly biconvex to subtrigonal; commissure uniplicate, fold moderately high, standing increasingly high anteriorly, beginning 1–5 mm anterior to brachial beak; sulcus rather shallow, but dipping steeply at anterior, extending forward as broad tongue, producing emargination of anterior. Costae strong and sharp crested on fold and in sulcus, lower, broader, and rounder on flanks, beginning at beaks, frequently bifurcated, especially on fold and sulcus, numbering 6–10 on fold (normally 9), one less in sulcus, 4–9 on each flank, number not necessarily equal on both sides; stolidium better developed on brachial valve, varying from broad and fanlike to nearly absent.

Pedicle valve flatly convex transversely and from beak to flanks, strongly convex longitudinally through sulcus; beak short, only moderately thick, suberect to erect but not hooked; beak ridges gently curved, ill-defined; lateral pseudointerareas elongate, narrow, normally covered by edge of brachial valve; delthyrium moderately large, sides only slightly constricted by small, normally widely disjunct deltidial plates; foramen large for genus, nevertheless small, opening ventrally.

Brachial valve strongly convex transversely, only moderately convex along crest of fold owing to anterior increase in height of fold, convexity uniform without swelling in umbonal region; beak bluntly pointed, apex only slightly inside pedicle valve.

Pedicle valve interior with small teeth, continuous with dental plates that form short, boat-shaped spondylium just above floor of valve; median septum low, extending slightly forward of spondylium; troughs of vascula media diverging from midline of valve just anterior to median septum, extending directly across floor of valve; muscle marks in spondylium faint and undifferentiated.

Brachial valve interior with short, broad hinge plate, semicircular to crescentic; cardinal process at apex of hinge plate, located just beneath apex of valve, low or rather high, knoblike, normally not polylobate, shallowly striate for muscle attachment; hinge sockets short, narrow, at lateral extremes of hinge plate, finely corrugated; crural bases slightly diverging anterior to cardinal process, space between filled by narrow crural plates dipping along center line attaching crural bases to top of intercamarophorial plate; brachial processes not observed, presumed to be normal for
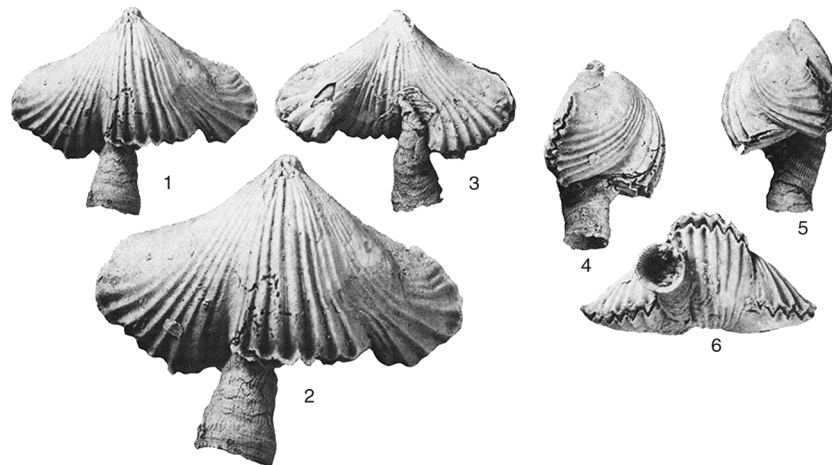

FIGURE 4.1 Permian brachiopod *Stenoscisma pyraustoides* **Cooper and Grant.** The original species description is printed in this box. The photographs are of the holotype (with a coral cemented to it). *(From Cooper & Grant, 1976)*

genus; median septum high, thin, exceptionally short, length increasing greatly with height; camarophorium narrow, relatively short, anteriorly widening; intercamarophorial plate low, thick, relatively long; muscle marks not observed.

STRATIGRAPHIC OCCURRENCE. Skinner Ranch Formation (base); Hess Formation (Taylor Ranch Member); Cibolo Formation.

LOCALITIES. Skinner Ranch: USNM 705a, 705b, ?709a, 711o, 711z, 715c, 716p, 720e, 726j, 729j. Taylor Ranch: USNM 716o. Cibolo: USNM 739-1.

DIAGNOSIS. Exceptionally large and wide *Stenoscisma* with numerous bifurcations of costae on posterior of fold and flanks.

TYPES. Holotype: USNM 152220i. Figured paratypes: USNM 152219a-d; 152220b,c,k; 152221a,b; 152225. Measured paratypes: USNM 152220a-h,j; 152225. Unfigured paratypes: USNM 152220a,d-h.j.

COMPARISONS. *Stenocisma pyraustoides* is characterized by its exceptional width, large maximum size, numerous and frequently bifurcating costae on flanks, short beak with small disjunct deltidial plates, relatively short spondylium and camarophorium.

The only known species that is closely related to *S. pyraustoides* is *S. multicostum* Stehli (1954, cited in Cooper & Grant, 1976) from the Sierra Diablo. *Stenoscisma pyraustoides* is larger, wider, and less strongly costate, especially on the flanks where the costae are lower, broader, and fewer. The species bears superficial resemblance to *S. trabeatum*, new species, which is smaller, more triangular in outline, less strongly convex, has a longer beak, and a stolidium that is continuous from flanks to fold.

TABLE 4.2

Measurements (in mm; measurements exclude stolidium)

Localities and Types	Length	Brachial Valve Length	Width	Thickness	Apical Angle (°)
USNM 705a					
152220a	13.0	10.7	14.5	circa 6.0	95
152220b	15.0?	13.0	16.7	10.3	89
152220c	13.5	12.8	18.4	11.0	104
152220d	18.2	16.2	23.5	14.0	103
152220e	19.0	16.8	26.0+	14.0	107
152220f	23.7	22.4	28.0	16.0	93
152220g	26.0	25.2	35.9	21.3	116
152220h	28.3	26.6	45.1	22.7	104
152220i (holotype)	32.5	30.5	50.0	26.6	114
152220j	34.7	32.5	56.0?	21.0?	118
USNM 716o					
152225	35.5	33.5	50.5	23.2	109

Box 4.2

DIPLOCAULUS PARVUS OLSON, N. SP.

HOLOTYPE. UCLA VP 3015, partial skull and skeleton including vertebrae, ribs, shoulder girdle, humerus, radius, and ulna. (See Figure 4.2 and Table 4.3.)

HORIZON AND LOCALITY. Chickasha Formation (Permian: Guadalupian, equivalent to the middle level of the Flowerpot Formation) about 2 miles east of Hitchcock, Blaine County, Oklahoma. Site BC- I (Olson, 1965; cited in Olson, 1972). SW 1/4 SW 1/4, sec.6, T. 17N., R. 10W., Blaine County, Oklahoma.

DIAGNOSIS. A small species of *Diplocaulus*, in which the adult ratio of skull length to skull width is attained when the skull length is approximately 60 mm, as contrasted to *D. magnicornis* and *D. recurvatus*, in which the adult ratio is reached at skull lengths of between 80 and 110 mm. Otherwise similar in all features to *D. recurvatus*. (See Figure 4.3.)

TABLE 4.3

Measurements of Skull Dimensions Based on UCLA VP 3015 (as described and figured in Olson, 1953; cited in Olson, 1972)

	mm
Skull length	63.0
Skull width	172.0
Pineal-frontal length	5.0
Interparietal length	14.1
Parietal length	19.6
Frontal length	25.2
Orbito-snout length	14.5
Interorbital width	10.8
Orbital width	10.2
Orbital length	9.9
Parietal width*	84.0
Interparietal width	94.0

* Based upon measurement of right-hand element and multiplied by 2 to give full width as used in various other papers.

FIGURE 4.2 **Permian amphibian *Diplocaulus parvus* Olson.** The original species description is printed in this box. The drawing is a dorsal view of the holotype. *(From Olson, 1972)*
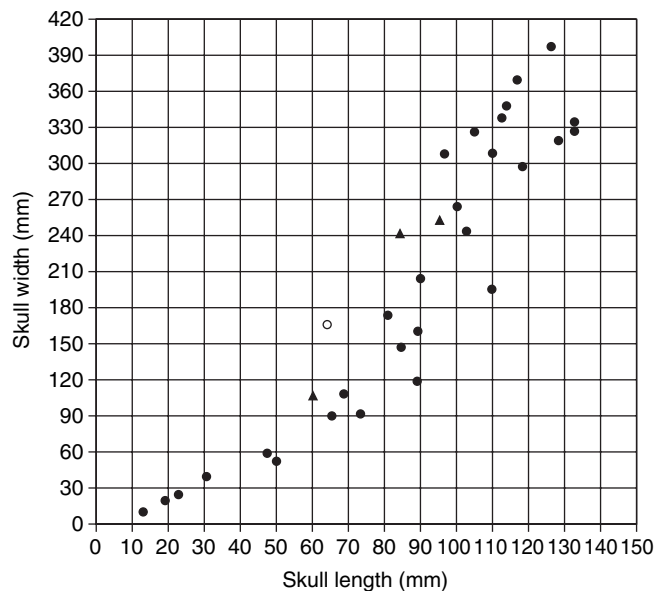

FIGURE 4.3 **The relationships of skull length and skull width in *Diplocaulus*.** Closed circles: *D. magnicornis*; open circles: *D. parvus*; triangles: *D. recurvatus*. *(From Olson, 1972)*

deposits, it was not until 1960 that a specimen was reported in which *Archaeopteris* was attached to *Callixylon*, making it clear that they were one and the same organism (Figure 4.6). This was important, as it demonstrated a previously unknown kind of plant—with wood like that known in seed plants but with branches that bear spores rather than the characteristic reproductive structures of seed plants.

Another case involves the **CONODONTA**—a primarily Paleozoic group of organisms known from characteristic toothlike elements made of calcium phosphate (Figure 4.7). It was generally thought, from shortly after the initial discovery of conodonts in the 1850s, that several different elements probably came from the same organism. Without clear evidence of this, however, a **form taxonomy,** which treats each element separately, was widely applied. Starting in the 1930s, the repeated discovery of particular assemblages of different conodonts, sometimes diagenetically fused, made it clear that several different elements must be part of the same organism. By the 1960s, therefore, form taxonomy had been largely abandoned in favor of a multielement taxonomy that tried to identify assemblages of conodonts belonging to the same species.

Finally, in the 1980s, several finds were reported of soft-bodied animals with bilaterally symmetrical assemblages of conodonts. Located in the pharyngeal region of the animal, the conodonts were evidently part of a feeding apparatus. This and many subsequent discoveries have revealed a number of characteristics of the soft anatomy that suggest the conodont-bearing animal was a **CHORDATE.**

Just as the question of what constitutes adequate material varies from case to case, there are differences from group to group in the attributes of organisms that are used in diagnosis. Such attributes are referred to as *taxonomic characters*. Despite these differences, any taxonomic character should satisfy several conditions. It must be a fairly obvious attribute, especially in fossil material in which shortcomings of preservation often yield an incomplete picture of the total organism. Nevertheless, in certain groups, sectioning or other procedures may be required to identify taxonomic characters. Ideally, a taxonomic character should be present and recognizable throughout an organism's ontogeny, and not just during certain growth stages. It should also show limited variation within a species. Characters should be avoided if they are known, from the study of living relatives, to show substantial ecophenotypic variation [SEE SECTION 3.1].

Presentation of Taxonomic Names

Formal taxonomic names appear in print for a variety of reasons: description of new species, taxonomic revision, inventory of species found in a sample, labeling of museum specimens, and so on. In any case, accurate communication requires that the names be presented in a standard form. By convention, the genus and species names are italicized when printed and underlined when written or typed. The genus name is capitalized and the species name is not. Immediately following the species name, the name of the author of the species is given.

The following (from Farrell, 1992) is an example of a typical fossil list, which helps to illustrate the conventions that surround the presentation of taxonomic names. Notice that the names of some authors of species are enclosed within parentheses, which indicates that the genus assignment has been changed since the species was erected. Notice also that a genus name may be abbreviated to its initial letter in a list of two or more **congeneric** species. This is acceptable as long as it is unambiguous. In the text of a paleontologic paper, genus names are often abbreviated and the names of authors of species deleted (see Boxes 4.1, 4.2, and 4.3).

Selected Fossils from the Garra Formation, Early Devonian, New South Wales

Dolerorthis angustimusculus n. sp. Farrell
Skenidioides sp. cf. *S. robertsensis* Johnson, Boucot, and Murphy
Muriferella sp. cf. *M. punctata* (Talent)
Iridistrophia mawsonae n. sp. Farrell
Eoschuchertella burrenensis (Savage)
Colletostracia roslynae n. gen. n. sp. Farrell
Gypidula pelagica austrelux n. subsp. Farrell
Grayina magnifica australis (Savage)
Machaeraria catombalensis Strusz
Atrypina sp. cf. *A. erugata* Amsden
Reticulatrypa fairhillensis Savage
Spirigerina (Spirigerina) supramarginalis (Khalfin)
S. (S.) marginaliformis Alekseeva
Megakozlowskiella sp.
Reticulariopsis sp.
Straparollus (Straparollus) sp.
Straparollus (Serpulospira) sp.
Hyalospongea indet.
Heliolites daintreei Nicholson and Etheridge
Pleurodictyum megastoma M'Coy
Calymenina indet.

Box 4.3

NAMACALATHUS HERMANASTES GROTZINGER, WATTERS, AND KNOLL, N. GEN. N. SP.

Genus *Namacalathus* n. gen.

TYPE SPECIES. *Namacalathus hermanastes* n. sp.

DIAGNOSIS. Centimeter-scale, chalice- or goblet-shaped fossils consisting of a calcareous wall less than 1 mm thick; a basal stem open at either end connects to a broadly spheroidal cup perforated by six or seven holes with slightly incurved margins distributed regularly around the cup periphery and separated by lateral walls; the cup contains an upper circular opening lined by an incurved lip.

ETYMOLOGY. From the Nama Group and the Greek *kalathos*, denoting a lily- or vase-shaped basket with a narrow base or, in latinized form, a wine goblet.

Namacalathus hermanastes n. sp.

DIAGNOSIS. A species of *Namacalathus* distinguished by cups 2–25 mm in maximum dimension, with aspect ratio (maximum cup diameter/cup height) of 0.8–1.5.

DESCRIPTION. Goblet-shaped calcified fossils; walls flexible, ca. 100 μm thick (original wall dimensions commonly obscured by diagenetic cement growth); basal cylindrical stem, hollow and open at both ends, 1–2 mm wide and up to 30 mm long, attached to spheroidal cup; cup with maximum dimension 2–25 mm, broad circular opening at top with inward-curving lip, perforated by six to seven slightly incurved holes

FIGURE 4.4 Tomographic reconstructions of the calcified fossil *Namacalathus hermanastes*. *(From Grotzinger et al., 2000)*
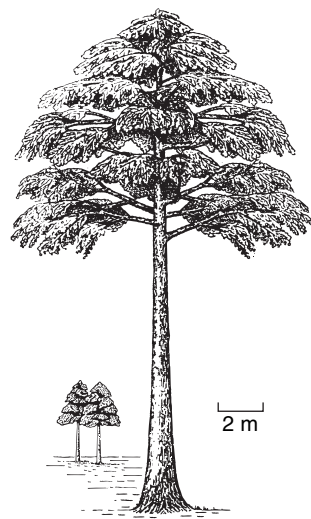

(a)

(b)

2 cm

2 m
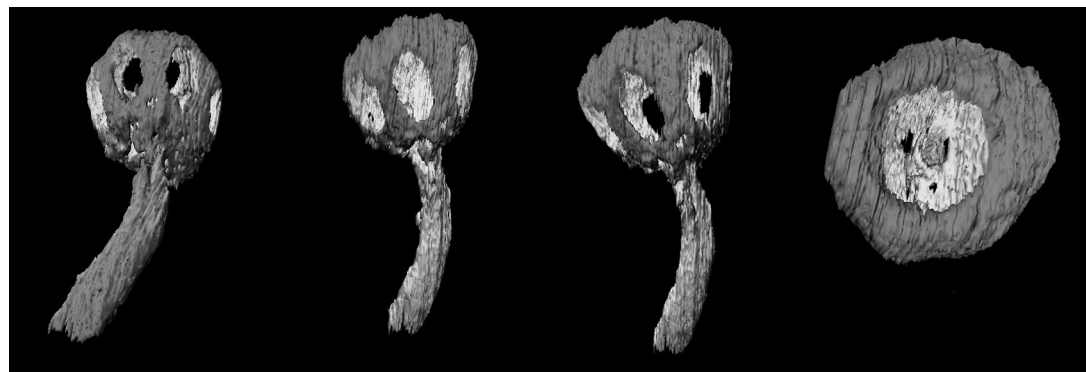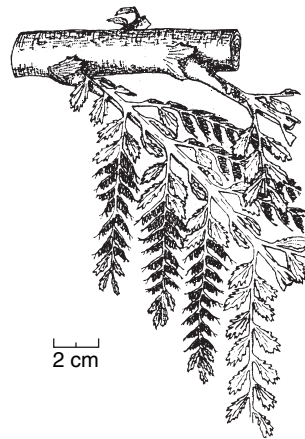
FIGURE 4.6 Reconstruction of the Upper Devonian land plant *Archaeopteris*. (a) A branch. (b) An entire tree. *(From Beck, 1962)*

of similar size and shape distributed regularly about cup periphery. Specimens preserved principally by void-filling calcite, with rare preservation of primary, organic-rich wall.

ETYMOLOGY. From the Greek *herma*, meaning "sunken rock or reef," and *nastes*, meaning "inhabitant."

MATERIAL. More than 1000 specimens from biohermal carbonates of the Kuibis and Schwarzrand Subgroups, terminal Proterozoic Nama Group, Namibia.

TYPE SPECIMEN. Our understanding of *Namacalathus hermanastes* derives principally from virtual fossils modeled from serially ground surfaces (see Figure 4.4). Systematic practice, however, requires that real fossils be designated as types. Accordingly, the specimen illustrated in the lower right corner of Figure 4.5 is designated as holotype for the species. The type specimen is to be reposited in the paleontological collections of the Museum of the Geological Survey of Namibia, as collection No. F314. Representative specimens are also housed in the Paleobotanical Collections of the Harvard University Herbaria (HUHPC No. 62989).

TYPE LOCALITY. Reefal biostrome developed at the top of the Omkyk Member, Zaris Formation, Kuibis
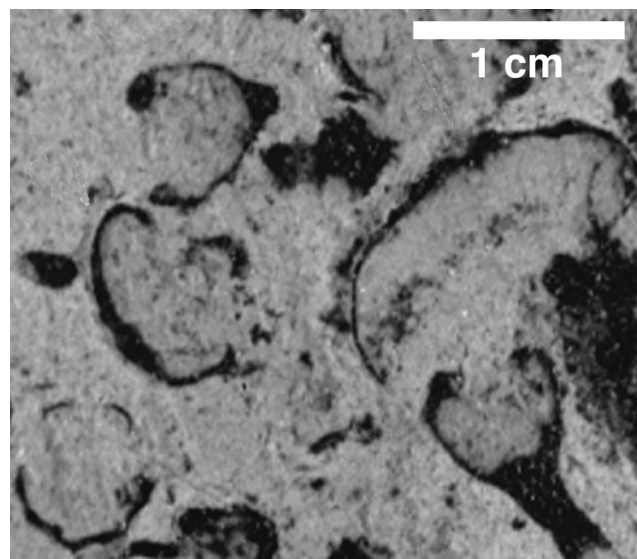

FIGURE 4.5 Assemblage of calcified *Namacalathus* fossils within reefal and related thrombolitic horizons within the Nama Group. Original goblet-shaped fossil described by Grotzinger et al. (1995; cited in Grotzinger et al., 2000). Note adjacent cup-shaped fossils, which also represent cross sections of *Namacalathus*.

Subgroup, exposed along the Zebra River near the boundary between Donkergange and Zebra River farms, south of Bullsport, Namibia.

In a number of entries in the list, the subgenus taxonomic rank is given, enclosed in parentheses and following the genus name (for example, *Serpulospira*). In a few cases, a subspecies name follows that of the species. An "sp.," rather than a species name, following a genus or subgenus name indicates that the species could not be identified with confidence. In a few cases, "sp." is followed by "cf." (for the Latin *confer*, compare) and a species name, indicating a questionable or doubtful species identification. A higher taxonomic name followed by "indet." indicates that identification could not be made below the level of the higher taxon. When "n. sp." follows a species name, this means that the author of the list is naming the species for the first time. A new genus is indicated by "n. gen."

Changing Species Names

A worker may change the name of a taxon either because its use violates a rule of nomenclature or because it is judged to be improperly classified. We will restrict our discussion of name changes to species names.

Homonyms are identical names that denote different species. There are two varieties. Primary homonyms are identical names that were erected for different taxa (with different holotypes) belonging to the same genus. The author of the later-named homonym was in error, not knowing that the species name had been occupied. Once such an error is discovered, only the first published, or senior homonym,
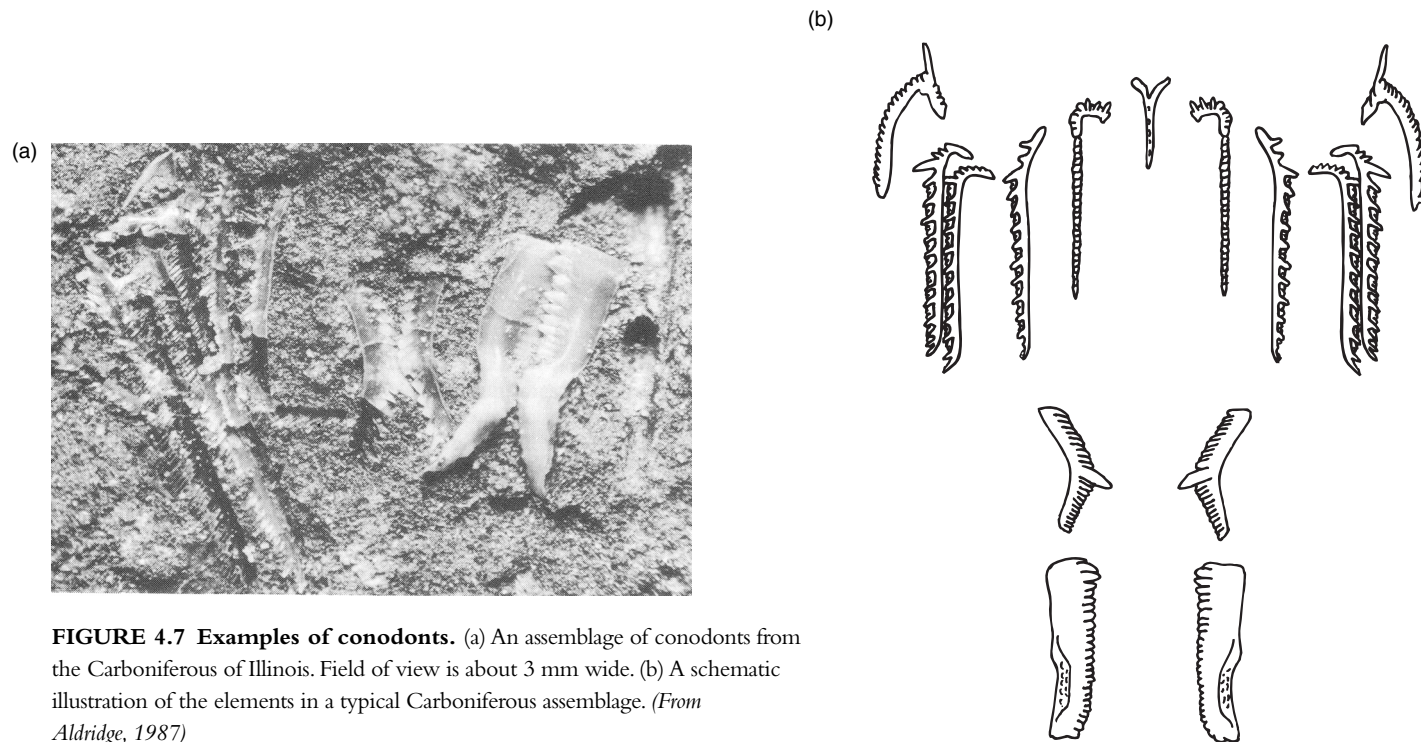
(b)

(a)

FIGURE 4.7 Examples of conodonts. (a) An assemblage of conodonts from the Carboniferous of Illinois. Field of view is about 3 mm wide. (b) A schematic illustration of the elements in a typical Carboniferous assemblage. *(From Aldridge, 1987)*

can be retained. The difference between primary and secondary homonyms is that the latter originate by transfer of one species to a new genus that contains a species with the same species name. The author of neither species is in error because the same species name can be used for species belonging to different genera. A primary or secondary homonym must be replaced by the oldest available name or, if no previously published name is available, by a new name.

Synonyms are two different names applied to the same taxon. There are two varieties. Objective synonyms are different names that are based on the same type specimen or specimens. Here there is no question of taxonomic opinion; the senior (first published) synonym must generally be retained, and the junior synonym must be permanently rejected. This is the law of **priority.** Subjective synonyms are names that were established for different type specimens that are later judged by a worker to belong to one species. Another worker, however, may judge that the type specimens belong to separate species; this worker will not consider the names to be synonyms and will retain both. In other words, while a junior objective synonym is eliminated automatically, a junior subjective synonym remains available as a name, its use depending entirely upon taxonomic opinion.

Rejection of names on the basis of priority is sometimes unfortunate because it eliminates familiar names and may make it difficult for future workers to trace older literature. The formal change in genus name of the familiar Eocene "dawn horse" from *Eohippus* to *Hyracotherium* was unpleasant to many workers. The Commission on Zoological Nomenclature, which administers the Code, is empowered to suspend the rule of priority at special request. Many familiar names found to be junior homonyms or synonyms have been retained by this procedure. Partly to relieve the Commission of the burden of taking numerous actions of this sort, the most recent edition of the Code empowers authors to choose common usage over priority in specific circumstances.

Box 4.4 gives an example of a list of taxonomic names known as a *synonymy*. A synonymy is a brief history of the taxonomic treatment of a species, with bibliographic citations to important works. Synonymies are important parts of new species descriptions as well as systematic revisions of higher taxa. This example is somewhat complicated but by no means unusually so. Because a synonymy is in part an historical record and in part an interpretation of a taxonomic situation, it is common that synonymies written by different specialists for a single species name do not agree.

Box 4.4

SYNONYMY OF *ARCHAEOCIDARIS ROSSICA*

The following synonymy was written by Robert Tracy Jackson (1912) for a Lower Carboniferous echinoid species. The heading indicates Jackson's opinion as to the valid species name and the genus to which it belongs: *Archaeocidaris rossica* (von Buch). (Note that Jackson refers to L. von Buch as *Buch*; current convention is to consider *von Buch* the surname.)

This species was first described by E. Eichwald in 1841 under the name of *Cidaris deucalionis*, but the name is disallowed by Jackson because Eichwald's description was too vague. The next entry is to von Buch's description of the species as *Cidaris rossicus*. As the first valid description of the species, the name *rossicus* has priority over all names subsequently applied to the species (although the spelling has been altered to conform grammatically to a change in genus affiliation).

The third entry in the synonymy records the assignment of the species to the genus *Cidarites* (meaning "fossil *Cidaris*") by R. I. Murchison, E. Verneuil, and A. Keyserling. Several subsequent entries record similar shifts in genus affiliation, most reflecting changes or differences of opinion regarding the taxonomic relationships of the species. One entry in the synonymy stands out from the others: *Echinocrinus deucalionis*. This is credited to Eichwald (1860), who evidently recognized as valid his 1841 publication of the name *Cidaris deucalionis*.

The use of the genus name *Echinocrinus* raises another nomenclatural problem. This name was proposed (quite validly) in 1841 by L. Agassiz. *Archaeocidaris* was proposed independently for the same group of echinoids three years later by F. McCoy (1844).

Technically, the name *Echinocrinus* is the correct name because it was proposed first. A special exception was made in 1955, however, by the International Commission on Zoological Nomenclature partly because *Echinocrinus* had rarely been used by echinoid specialists and partly because it was misleading in being very similar to genus names common in nonechinoid echinoderms (particularly crinoids).

Archaeocidaris rossica **(Buch)**

(?)*Cidaris deucalionis* Eichwald, 1841, p. 88. [Description is unrecognizable so the name cannot hold.]

Cidaris rossicus Buch, 1842, p. 323.

Cidarites rossicus Murchison, Verneuil, and Keyserling, 1845, p. 17, Plate 1, figs. 2a–2e.

Palaeocidaris rossica L. Agassiz and Desor, 1846–1847, p. 367.

Echinocrinus rossica d'Orbigny, 1850, p. 154.

Palaeocidaris (Echinocrinus) rossica Vogt, 1854, p. 314.

Eocidaris rossica Desor, 1858, p. 156, Plate 21, figs. 3–6.

Echinocrinus deucalionis Eichwald, 1860, p. 652.

Eocidaris rossicus Geinitz, 1866, p. 61.

Archaeocidaris rossicus Trautschold, 1868, Plate 9, figs. 1–10b; 1879, p. 6, Plate 2, figs. 1a–1f, 1h, 1i, 1k, 1l; Quenstedt, 1875, p. 373, Plate 75, fig. 12; Klem, 1904, p. 55.

Archaeocidaris rossica Lovén, 1874, p. 43; Tornquist, 1896, text fig. p. 27, Plate 4, figs. 1–5, 7, 8.

Archaeocidaris rossica var. *schellwieni* Tornquist, 1897, p. 781, Plate 22, fig. 12.

Cidarotropus rossica Lambert and Thiéry, 1910, p. 125.

Importance of Taxonomic Procedure

The importance of proper taxonomic procedure cannot be overstated. Adequate description and designation of types ensure that other workers know what an author had in mind when erecting a new species. Strict adherence to rules of nomenclature and to accepted conventions of reporting taxonomic names is necessary for communication. It is as important for paleontologists to use the name *Tyrannosaurus rex* consistently as it is for chemists to apply

the name *hydrogen* to one and only one element, or for mathematicians to recognize that the number π is a constant. The name in a sense takes on a life of its own.

Proper and consistent reporting is especially important when large inventories of fossil species are compiled for studies of ecology, evolution, and geology. Earlier in this section, we presented a partial list of taxa identified from a Lower Devonian formation in Australia. This is but one of the tens of thousands of similar lists that have been collated into electronic databases for purposes of

paleontological analysis. We discuss such databases else-where in this book [SEE SECTION 8.7]. For now, it is im-portant to note two points. First, keeping proper track of species names and their authors potentially saves great effort by allowing future taxonomic revisions to be au-tomatically applied to a compilation. Second, the user of such a compilation is unlikely to go back to each origi-nal list and verify that the list as represented in the data-base is faithful to the author's intentions.

Consider the brachiopod identified as *Skenidioides* sp. cf. *S. robertsensis* on the list of Devonian fossils. The species *S. robertsensis* itself is known from deposits of roughly the same age in Nevada and Arctic Canada. If the Australian occurrence of *S.* sp. cf. *S. robertsensis* had been inadvertently entered into the database as *S. robertsensis*, this could easily mislead the user into thinking that this species is known with confidence from a much broader geographic distribution than is in fact the case.

The example of *Skenidioides* is but a minor instance of the kinds of problems that can arise if names are not re-ported accurately. In one sense, this situation is no dif-ferent from the publication of a synonymy or taxonomic revision—where we are likely to accept an author's sum-mary of how previous authors used a name. But in an-other sense, there is a fundamental difference. One could in principle verify every entry in a typical synonymy, such as that in Box 4.4. Given the scale of many sec-ondary taxonomic compilations, however, such verifica-tion could not even be contemplated. It is therefore necessary to take steps to minimize errors when com-piling taxonomic names.

4.2 PHYLOGENETICS

Many areas of paleontology depend on knowing the evolutionary or genealogical relationships among species and among more inclusive groups. These include hetero-chrony [SEE SECTION 2.3], rates of evolution [SECTION 7.1], and evolutionary trends [SECTION 7.4]. **Phyloge-netics** is the enterprise that attempts to deduce evolu-tionary relationships. This field is distinct from **classification,** the organization of species into a hierar-chical system of named categories. Phylogenetics and classification are linked, because most workers prefer a system of classification that reflects inferred phylogeny in some way. Nonetheless, even if one knew the evolu-tionary relationships among species, there could be nu-merous alternative classifications that legitimately reflect these relationships.

In this section, we present some of the simplest meth-ods that illustrate the logic by which evolutionary relationships are estimated. We do not treat the analysis of DNA sequences and other molecular data that are generally available only for living organisms. Such data are essential for biologists, however, and students should consult the references listed at the end of this chapter to become familiar with the analysis of molecular data.

Cladograms and Trees

Because all species living today and all those known from the fossil record are descended from a single origin of life, all species are related to some extent. For many purposes, it is useful to focus on the most proximal rela-tionships between species and to distinguish two funda-mental patterns of relationship. First, one species may be ancestral to another, descendant species, either directly or via intermediates. Second, two species may merely share a common ancestor.

Figure 4.8 portrays relationships for a small group of hypothetical species in the form of a **cladogram** (from the Greek *klados*, branch). This is a branching diagram that portrays proximity of relationship without a tem-poral dimension. The points where branches join are **nodes.** The information in this cladogram can be por-trayed in other ways, such as by nested parentheses, as follows: ((AB)C)(DE). Although a cladogram does not
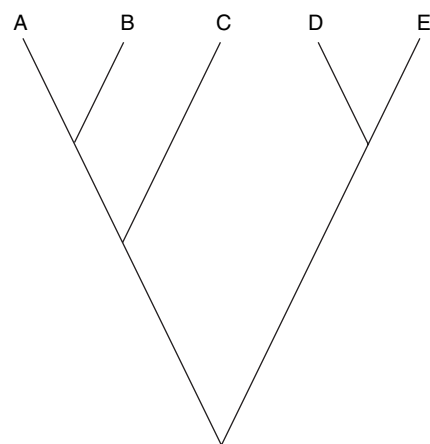

FIGURE 4.8 Cladogram showing relationships among five hypothetical species. Species A and B are mutually most closely related, as are D and E. Species C is more closely related to A and B than to D and E.

explicitly portray time, the association of species A and B implies that they share a common ancestor more recently in time than either does with any of the remaining species. In this sense, A and B are mutually most closely related. The same is true of D and E. Together, A and B share a more recent common ancestor with C than any one of A, B, or C does with either D or E. By definition, A and B are **sister species,** as are D and E. Two or more species that share a common ancestor, together with all the other descendants of that common ancestor, are said to form a **clade.** Species A and B form a clade, as do D and E. The groupings (AB)C and ((AB)C)(DE) are also clades. Just as A and B are sister species, (AB)C and DE are **sister clades.** The node linking two sister species or sister clades represents the common ancestor to them.

We must distinguish this cladogram from numerous **evolutionary trees** that are consistent with the pattern of relationships in the cladogram. Evolutionary trees portray ancestral–descendant relationships over actual time and can also depict other aspects of evolution, such as morphological change. Although we commonly speak of relationships among species and other taxa, in general only *samples* of lineages are available, sometimes referred to as **lineage segments.** For paleontologists, these are populations from particular localities and stratigraphic horizons. For biologists, they are populations that happen to be alive today.

Figure 4.9 shows the temporal positions of the five hypothetical species of Figure 4.8, along with two of many possible evolutionary trees consistent with the cladogram. In the first of these trees (Figure 4.9b), some sampled species occupy an ancestral position. Species C gave rise to the common ancestor of A and B, and D gave rise to E. The "species" D and E are in fact two samples or segments of the same lineage. In the other tree (Figure 4.9c), all the species are linked through unsampled common ancestors, and each sample represents a distinct lineage. A species or lineage segment that does not give rise to any descendants is said to be **terminal.** A, B, and E are terminal in Figure 4.9b, and all lineage segments are terminal in Figure 4.9c.

Our earlier discussion of the process of speciation [SEE SECTION 3.3] emphasized the splitting of an evolutionary lineage into two separate lineages. This still leaves the question of whether either of the two resulting lineages should be regarded as ancestral to the other. If speciation occurs via the attainment of reproductive isolation in a population that is separate from the main geographic
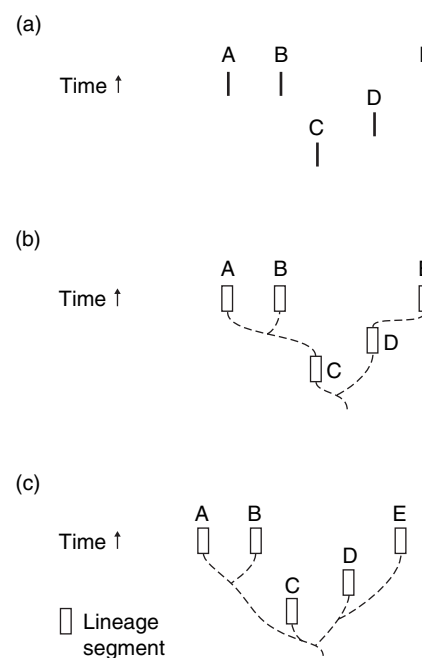

FIGURE 4.9 **Illustration of lineage segments.** (a) Temporal position of the five sampled parts of lineages (lineage segments) shown in the cladogram of Figure 4.8. (b, c) Two of many possible evolutionary trees corresponding to this cladogram. Dashed lines show lines of descent between lineage segments. In part (b), lineage segments C and D are ancestral to others. In part (c), all sampled lineages are terminal.

range of the species, then it is straightforward to consider the species in the main range as the ancestor. It may be that one of the two lineages exhibits less evolutionary change than the other [SEE SECTION 7.3]. In such a situation, it is conventional to regard the more static lineage as the ancestor and the more divergent one as the descendant.

We discuss the construction of cladograms and trees later in this chapter. For now, consider an actual example of each to see some of their main features. Figure 4.10 presents a highly simplified cladogram for selected tetrapod vertebrates. Each branch may represent numerous species. On this figure, the tick labeled *T* marks the evolution of a set of features that define tetrapods to the exclusion of other vertebrates; these include details of bones and their arrangement in the forelimb, hindlimb, and vertebral column. The ticks show the evolution of additional characters, such as the amniote egg (*a*), mammary glands (*m*), and wings (*w*). These are not necessarily taxonomically diagnostic characters.

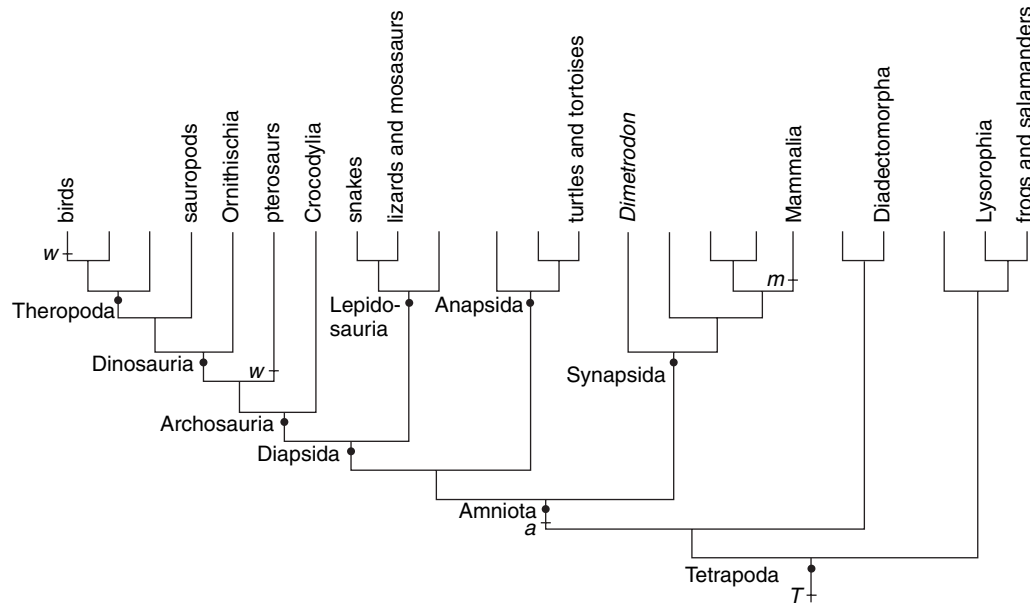An evolutionary tree of tetrapods, consistent with the cladogram of Figure 4.10 but even further simplified, is

FIGURE 4.10 Highly simplified cladogram of tetrapod vertebrates with the evolution of selected characters indicated. Selected branches, mostly familiar groups, are labeled. Unlabeled branches represent less familiar groups. Names in uppercase letters are scientific names; others are common names. The *T* denotes a number of skeletal characters of the limbs and vertebral column that characterize tetrapods. Other characters shown are the amniote egg (*a*), mammary glands (*m*), and wings (*w*). The names of selected clades appear at nodes. All the taxa that diverge from a node are in the named clade.
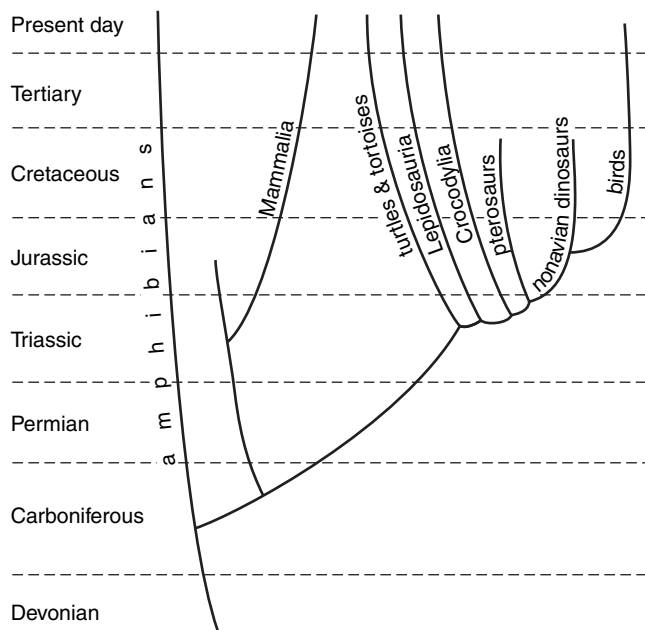

FIGURE 4.11 Highly simplified evolutionary tree of tetrapods, showing some of the main lineages in the cladogram of Figure 4.10.

given in Figure 4.11. The time of origin of groups is based both on their time of appearance in the fossil record and on the branching sequence of the cladogram. For example, lepidosaurs, crocodylians, pterosaurs, and dinosaurs first appear in the Triassic, but the order in which they appear is not the same as the order of branching of the cladogram. For Figure 4.11, the cladogram is used to establish the relative time of origin of these groups.

Shared Novelties and Evolutionary Relationships

To understand phylogenetic inference, it is helpful to start with a case in which we think we know the true evolutionary relationships. This will enable us to discern what kind of information would be useful if we had to reconstruct the cladogram, or tree, given only this information.

Assume for the sake of argument that the cladogram of Figure 4.10 is correct. We first distinguish between a **homologous** trait (one that is shared, with possible

modification, in two or more species because they inherited it from a common ancestor) and an **analogous** or **convergent** trait (one that is shared in two or more species whose lineages evolved it independently). According to the cladogram of Figure 4.10, the amniote egg is homologous in all the amniote tetrapods, and lactation is homologous in mammals. The wing, by contrast, evolved independently in the pterosaur and bird lineages, so it is convergent in those two groups. Thus, by their very nature, homologous characters carry information on proximity of evolutionary relationship, whereas convergent characters do not.

Determining whether similar traits are homologous has long been one of the most important and difficult tasks in biology. Detailed structural similarity, similarity of embryological unfolding of the trait, and tracing of evolutionary transitions through well-documented fossil sequences are among the most important clues to homology. Whether a trait is homologous depends to some extent on the scale of analysis. The bird and pterosaur forelimbs are not homologous as wings—the common ancestor of these two groups did not have wings—but they are homologous as forelimbs.

In the case of the pterosaur and bird wings, the modification of the forelimb is radically different in the two groups. The digits represent a good example. In pterosaurs, the first three digits are of normal size, the fourth digit is greatly elongated and supports the membranous wing, and the fifth digit is absent (Figure 4.12). In the oldest known bird, *Archaeopteryx*, there are three fully and essentially equally developed digits—the condition inherited from dinosaurs (Figure 4.13). (It should be noted here that modern birds possess numerous skeletal specializations not found in *Archaeopteryx*.)

Whether a homologous character is informative about evolutionary relationships depends on the scale of analysis. Consider the amniote egg. It is a **derived character** or **novelty** in vertebrate evolution that apparently evolved in the common ancestor of mammals, birds, and reptiles. Thus, when we consider the relationships among major vertebrate groups, the amniote egg is useful in uniting these three into a natural group, the **AMNIOTA,** to the exclusion of amphibians and other vertebrates. Within the Amniota, however, this character is primitive; all lineages share this character by inheritance from their common ancestor. Although the character is homologous, it gives no information that would allow us to determine that any pair among, say, birds, lizards, crocodiles, and mammals is most closely related to the exclusion of the other groups.
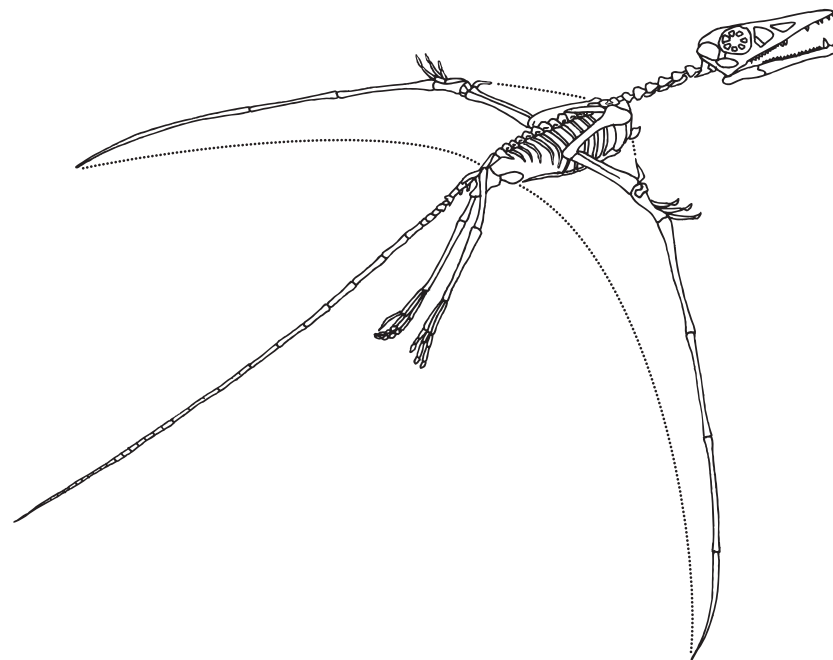

FIGURE 4.12 Skeletal reconstruction of the primitive pterosaur *Eudimorphodon* from the Late Triassic of Italy, showing the modified forelimb characterized by a very elongate fourth digit. *(From Carroll, 1988)*
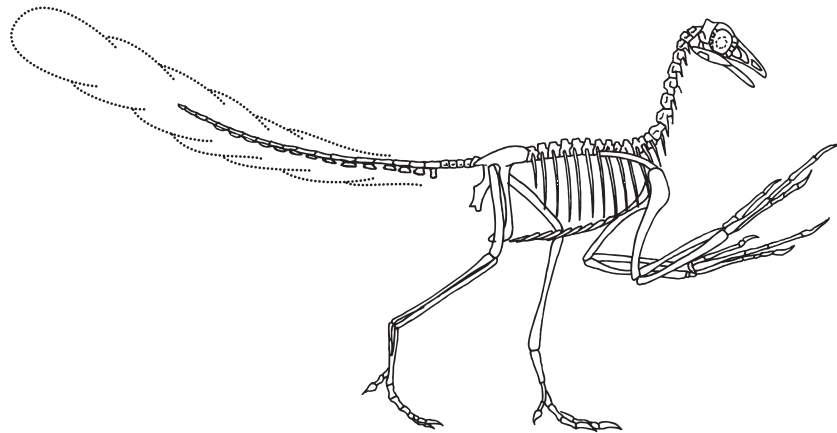
FIGURE 4.13 Skeletal reconstruction of *Archaeopteryx*, the oldest known bird, from the Late Jurassic of Germany, showing three elongate digits. *(From Carroll, 1988)*

As this case illustrates, the key to phylogenetic inference is to find characters that are homologous and novel at the appropriate scale of analysis. Homology tells us that a group of lineages shares a character by evolutionary descent. Novelty tells us that the lineages within the group share this character to the exclusion of some other lineages and are thus most closely related. Novel traits are referred to as **apomorphies** (*apo-*, away from), and primitive traits are **plesiomorphies** (*plesio-*, near). A novel character that is shared by a group of lineages is a **synapomorphy,** while one that is unique to a particular lineage is an **autapomorphy.**

In summary, synapomorphies are the key characters that allow us to deduce that groups of lineages are most closely related in the sense of sharing a common ancestor to the exclusion of other lineages.

Deep Homology   The example of convergence between the bird and pterosaur wings is one in which the pathways of evolution and resulting structures are profoundly different. There are other cases, however, in which convergently evolved traits represent repeated evolution along similar pathways from a similar starting condition. An example is found in bivalve molluscs, such as mussels, that are attached as adults via a specialized tuft of filaments called the *byssus* (Figure 4.14). Several bivalve lineages have independently evolved this style of attachment. As it happens, many
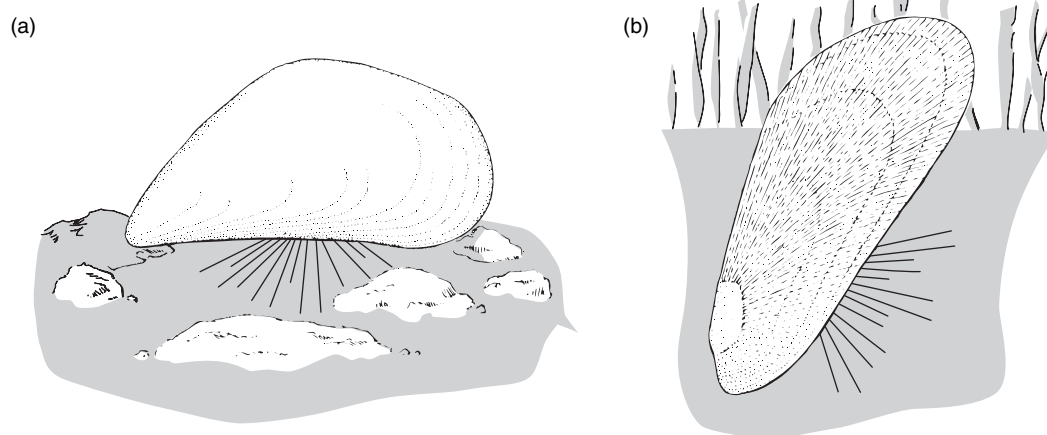

FIGURE 4.14 Examples of living bivalves that are bysally attached as adults. (a) *Mytilus*, which attaches to rocks and other firm substrates. (b) *Modiolus*, which attaches to debris within the sediment and is mostly buried within it. (*From Stanley, 1972*)
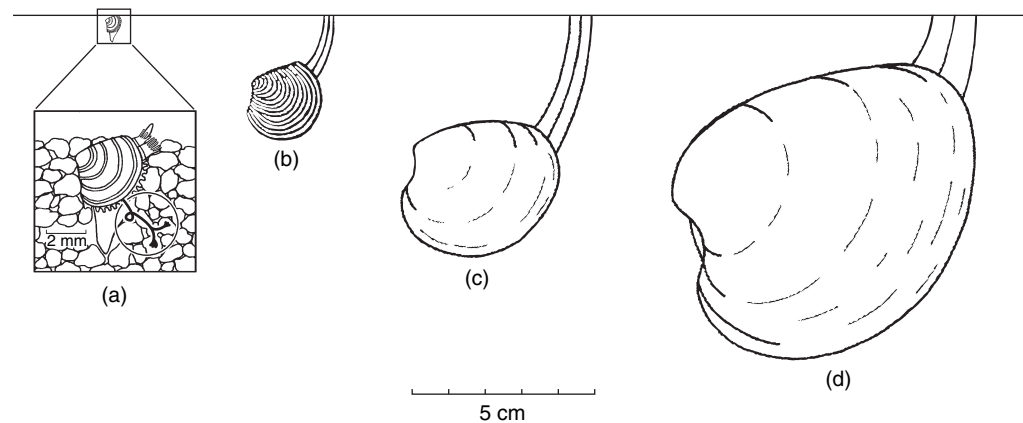
FIGURE 4.15 Ontogenetic stages in the living bivalve *Mercenaria mercenaria*, which lives within the sediment. (a) The very young juvenile is stabilized by byssal threads (circled). Subsequent stages lack byssal threads and are stabilized by (b) sharp ornamentation or by (c, d) sheer size. The organ extending to the sediment–water interface is the siphon, through which water is drawn and expelled for feeding and respiration. *(From Stanley, 1972)*

bivalve taxa that are not attached as adults, such as the common quahog *Mercenaria mercenaria* (Figure 4.15), have an early stage that remains stable in the sediment by using byssal threads. It is thought that the independent evolution of the adult byssus in various lineages may represent repeated instances of the retention of this juvenile condition via paedomorphosis [SEE SECTION 2.3].

In a similar vein, developmental genetics has revealed many cases of convergently evolved features deriving in part from similar genetic pathways in different lineages. To take just one such feature, the limbs of arthropods and vertebrates are clearly independently derived; the common ancestor to arthropods and vertebrates did not even have limbs. Yet both groups utilize a set of homologous genes, known as *Hox* genes, that set up the patterning of the body, including the limbs, during ontogeny. The ability of certain genes to establish patterning is apparently a homologous feature, but exploitation of these genes to produce limbs occurred independently in the arthropod and vertebrate lineages.

This phenomenon—in which structures have evolved independently in different lineages but nonetheless arise in ontogeny through the action of homologous genes—has been referred to as **deep homology.** Another example concerns eye development. Eyes have evolved numerous times independently in animals, yet many groups that have been studied use some of the same critical genes to produce eyes during ontogeny. In these examples, the shared genes are homologous characters, but the phenotypic structures—the limbs and eyes—are convergent.

Inferring Relationships from Morphological Characters

We just showed, with reference to an assumed evolutionary tree, that synapomorphies are the key to inferring evolutionary relationships. In reality, of course, we are not given the true evolutionary tree. We have species on which we can make anatomical observations, allowing us to specify a number of traits or characters, and that we may be able to date stratigraphically. Given such information, how does phylogenetic inference proceed?

One way to approach this problem is to start by establishing the **polarity** of characters, whether they are primitive or derived. Several criteria can be used to determine polarity. None is foolproof, and it is best to use several of them together.

1. *Outgroup comparison.* If a character varies within a group of interest, the state of the character in a related group is generally assumed to be primitive. The group of interest is referred to as the **ingroup** and the related group is called the **outgroup.** Referring back to our tetrapod example, mammals vary in the mode of birth, some being born live and some hatching from eggs. By comparing mammals with other tetrapods, we infer that egg-laying is primitive for mammals, because the primitive members of other tetrapod groups lay eggs. Outgroup comparison is the most common method of polarizing characters. It is best used when the outgroup is known to be reasonably close to the ingroup, so that one can have

confidence in homology of characters. Thus, some degree of prior phylogenetic analysis underlies the designation of outgroups.

2. *Stratigraphic position.* We expect traits appearing earlier in history to be primitive, on average, relative to later-appearing traits. Of course, the fossil record is incomplete, so this is a statistical rather than an absolute statement. It is especially important to be cautious with this criterion in cases where the acquisition of a character greatly affects preservation potential. Consider vascular plants, for example. Vascular plants are thought on good grounds to be derived relative to nonvascular plants, yet they have a richer early fossil record. This is evidently because the evolution of vascular tissue enhanced the preservability of land plants. As a consequence, a number of novelties within land plants appear in the fossil record before the primitive states.

3. *Developmental biology.* Traits that appear earlier in ontogeny are often interpreted as primitive relative to traits that appear later. For example, sharks and their relatives have a cartilaginous skeleton throughout life. Bony fishes, on the other hand, have a cartilaginous skeleton early in ontogeny, and this later ossifies. The cartilaginous skeleton would therefore be interpreted as the primitive state. It should be kept in mind, however, that the order of appearance of traits can be reversed, and that developmental stages can be lost altogether.

Let us suppose that we have a set of polarized characters for a number of species and that we wish to infer the evolutionary relationships among these species, expressed as a cladogram. Consider the simple data matrix of Figure 4.16a, which shows five species and

five polarized characters, with zero being the primitive state in each case. Let us propose some alternative cladograms and see what they imply about the evolution of certain traits.

One of many possible cladograms is shown in Figure 4.16b. This one implies five evolutionary transitions: the acquisition of the novel state of character 1 in the common ancestor to A through D; the acquisition of novelty 2 in the common ancestor to A and B; the acquisition of novelty 3 in the common ancestor to C and D; and the acquisition of novelties 4 and 5 in the lineages leading up to B and D, respectively. Note that the number of evolutionary transitions implied by this cladogram is equal to the number of derived character states.

Figure 4.16c shows another possible cladogram. Compared with the first cladogram, there are two main differences in implied character evolution: (1) Novelty 3 evolved twice—once in the lineage leading up to C and once in the lineage leading up to D; and (2) novelty 2 evolved in the common ancestor to A, B, and C, but this character subsequently reverted to the primitive state in the lineage leading up to C. Thus, there are seven rather than five implied evolutionary steps.

Given that both of these cladograms (and numerous others that could be constructed) are perfectly consistent with the character data, which should we prefer? One reasonable way to think of this problem is as follows: We have not in fact *observed* evolutionary transitions directly. Rather, we are *postulating* them as a means of explaining the character data. That is, we are suggesting each transition as a hypothesis. Each hypothesis is proposed to explain a particular subset of data that results from an unobserved evolutionary process. There is a strong intuitive appeal to favoring simpler explanations
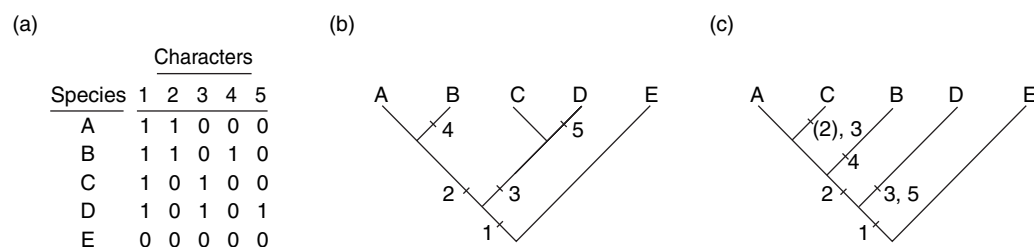

FIGURE 4.16 Example of cladogram construction. (a) Character data: 0 is the primitive state and 1 the derived state for each character. (b) Cladogram preferred on the basis of parsimony. This implies that each derived character state, denoted by the tick marks, evolved exactly once. (c) According to this alternative cladogram, derived character 3 evolved twice and character 2 reverted to the primitive state, as denoted by the character number in parentheses.

for data when more complex explanations are not needed. Thus, all else being equal, the first cladogram, with only five postulated evolutionary transitions, is preferred to the second one, with seven postulated transitions.

The cladogram that requires the fewest postulated character transitions to explain the observed character data is said to be most **parsimonious.** The number of transitions is commonly referred to as the *length* of the cladogram. Thus, the shortest cladogram is preferred by parsimony. Parsimony and cladogram length are discussed in more detail in Box 4.5.

It is important to bear in mind that parsimony is generally used as a scientific operating principle; we are not assuming that evolution in fact proceeds in such a way that the number of character transitions is minimized. Strict considerations of parsimony can and should be overturned when there are compelling reasons to do so. For example, sheetlike, or laminate leaves—as opposed to needles, scales, and other structures—appear in many groups of land plants. These include the progymnosperms (Figure 4.6), **SEED PLANTS** (Figure 2.6), **SPHENOPSIDS,** and **FERNS.** Although the relationships among these groups are not fully understood, enough is known about relationships *within* the groups to say with confidence that species with laminate leaves are nested within clades, the primitive members of which did not have laminate leaves. Therefore, laminate leaves must have evolved independently several times.

In light of this, a proposed genealogy that invokes several acquisitions of laminate leaves is not so unparsimonious as might be suggested by character data that simply scored such leaves as "absent" versus "present." In practice, the various laminate leaves could be coded as different characters to indicate the prior evidence that they are not in fact homologous, provided that one has reasonable confidence in this prior evidence.

Finding the most parsimonious cladogram is a computational problem in which every possibility must be explicitly evaluated before one can be sure that a more parsimonious solution does not exist. The examples treated here are simple enough that they can be solved by inspection. Most real studies, however, involve many species and characters, so that an exact, manual evaluation of all possible cladograms is not feasible. Many computer programs have therefore been written to facilitate the job of finding one or more cladograms that are maximally parsimonious. In fact, for more than a handful of taxa, the number of cladograms that must be considered is so large that they cannot all be evaluated even by a computer. Many algorithms have therefore been developed to find approximate solutions.

For simplicity, we have outlined the inference of evolutionary relationships starting with polarized characters. In fact, polarity is often determined after the phylogenetic analysis is done, as outlined in Box 4.6. For paleontologists and biologists interested in understanding evolutionary events as they actually occurred, polarity is of the utmost importance. If one is interested only in the topology of relationships (see Figure 4.18c in Box 4.6), however, it is not necessary to know character polarity.

Our treatment of phylogenetic inference implicitly assigns equal weight to all characters. The number of characters supporting each possible union of species is simply tabulated (Box 4.5), irrespective of anything we might know of these characters, such as their functional significance, or their tendency to revert from the derived to primitive state or to be attained convergently multiple times. In principle, a character that is thought to be less prone to evolve convergently or to revert to the primitive state would be given more weight. Rational weighting schemes, while quite desirable, have been elusive. Phylogenetic analysis therefore usually proceeds, at least in the initial stages, with equal weighting of characters.

The problem of character weighting is inherent in one of the fundamental assumptions underlying much of phylogenetic analysis. By assigning equal weight to every character, we are tacitly assuming that characters evolve independently. But this assumption is unlikely to be met in reality, if for no other reason than that many traits are under common genetic control [SEE SECTIONS 2.3 AND 3.2]. Moreover, several traits may evolve in concert because of an evolutionary modification in the way of life.

Earlier we mentioned the case of byssal attachment in bivalves. Within this style of attachment are two major categories: endobyssate (Figure 4.14b), in which most of the organism is within the sediment, and epibyssate (Figure 4.14a), in which the organism is attached on the surface of the substrate. The epibyssate condition, exemplified by the living mussel *Mytilus*, is more derived. For functional reasons, this condition is correlated with other modifications. These include the flattened ventral side of the shell, which confers stability by allowing close attachment to the substrate, and details of the musculature, which allow the byssus to be pulled tightly in a direction at right angles to the substrate. Thus, at least three traits—the adult byssus,

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Box 4.5

CHARACTER DISTRIBUTION
AND INCONSISTENCIES IN DATA

Another way to illustrate phylogenetic inference is to consider patterns of **character distribution** and what they tell us about relationships among species. In the example of Figure 4.16, character 1 has the pattern 1 1 1 1 0, meaning that it has state 1 in species A through D and state 0 in species E. The remaining characters have the patterns 1 1 0 0 0, 0 0 1 1 0, 0 1 0 0 0, and 0 0 0 1 0, respectively. Each cluster of 1s denotes a shared derived character state, which, as we have already stated, supports the association of one or more species to the exclusion of the others. Thus, character 1 implies that species A through D are mutually more closely related to each other than any of them is to species E, although this character permits no finer resolution of the relationships among A through D. Similarly, character 2 unites A and B, and character 3 unites C and D.

Characters 4 and 5, while they allow diagnosis of species B and D, respectively, are present in the derived state in only one species each, and therefore do not unite any species as most closely related. The constraints implied by these character distributions, when taken as a whole, yield the exact pattern of relationships expressed in the preferred cladogram of Figure 4.16b. We see that finding the arrangement of species that is supported by more character distributions than any other arrangement is exactly equivalent to finding the cladogram with the fewest implied evolutionary steps.

In the example of Figure 4.16, the smallest number of steps needed to explain the character data is exactly equal to the number of derived character states in the data. In general, the number of derived states is the same as the theoretical minimum length that the cladogram could have. A cladogram with this minimum length is one in which none of the associations of species implied by a character distribution conflicts with any of the others. For instance, character 2 in Figure 4.16 leads us to associate species A and B, and there are no traits that would lead us to associate either of these species with any of the remaining ones. In other words, stating that there are no conflicting interpretations of how char-

acter data lead to associations of species is equivalent to stating that the cladogram has the theoretically smallest number of steps.

In reality, paleontologists study tens to hundreds of characters, each with a different evolutionary history. It is therefore all but inevitable that they will show some conflict or **incongruence.** The most parsimonious cladogram is the one with a grouping of species supported by more characters than any other grouping. For example, Figure 4.17a shows a case in which there are five species and seven polarized characters. Character 1 unites A through D, and no other characters are in conflict with this union (Figure 4.17b). Characters 2 and 3 unite A and B to the exclusion of all other species, and characters 5 and 7 unite C and D to the exclusion of all others. Yet two conflicts affect the strength of support for the union of A with B and that of C with D. Character 4 unites A and C, and character 6 unites B and D. In this case, the unions of A with B and of C with D are each supported by two characters. Therefore, the conflicting arrangements (A + C and B + D), each supported by only one character, are overruled by the available evidence.

Figure 4.17c shows the most parsimonious cladogram consistent with these character distributions. Note that, because of the two character conflicts, there are nine steps on the cladogram—the evolution of characters 1, 2, 3, 5, and 7, and the evolution of characters 4 and 6 twice each—rather than the theoretical minimum of seven that would be expected if there were no conflicts among different characters.

In real examples, we are generally not so fortunate as to have character data that unambiguously support one cladogram over all others. Suppose, for example, that characters 2 and 7 were absent from the foregoing example. Then there would be exactly one character supporting each of the unions A + B, A + C, B + D, and C + D. As a result, there would be two rather different, but equally parsimonious, cladograms, each with seven evolutionary steps (Figure 4.17d).

A standard approach to the problem of multiple, equally parsimonous cladograms is to enumerate

them, if possible, and extract the features that they have in common. The character data in this example would not enable us to say with confidence which pairs of species are most closely related, but these data would argue that neither B + C nor A + D is a good candidate for a pair of sister species.
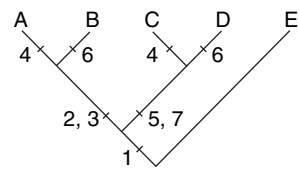
(a)

	Characters						
Species	1	2	3	4	5	6	7
A	1	1	1	1	0	0	0
B	1	1	1	0	0	1	0
C	1	0	0	1	1	0	1
D	1	0	0	0	1	1	1
E	0	0	0	0	0	0	0

(b)

(c)
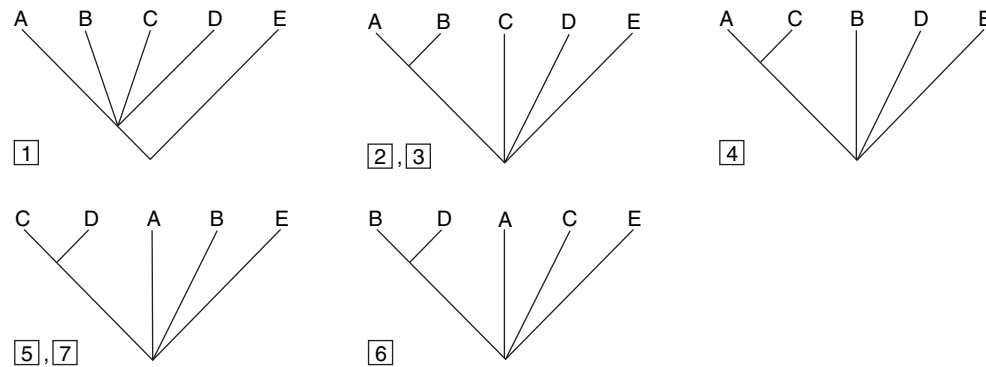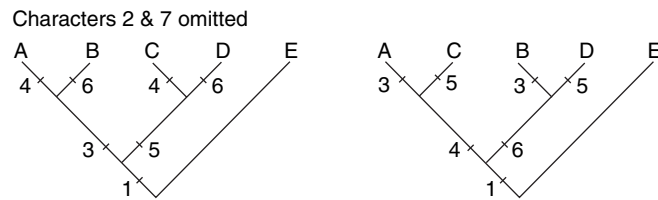
(d) Characters 2 & 7 omitted

FIGURE 4.17 Example of cladogram construction by finding associations of species supported by the maximal number of characters. (a) Character data: 0 is primitive and 1 is derived. (b) Cladograms implied by each of the seven characters. For example, character 1 unites A through D to the exclusion of C but allows no finer resolution, and characters 2 and 3 unite A and B to the exclusion of C, D, and E. (c) Cladogram for all characters. (d) Two equally parsimonious cladograms that would result if characters 2 and 7 were omitted.

Box 4.6

PHYLOGENETIC INFERENCE WITH UNPOLARIZED CHARACTERS

Consider the hypothetical example of Figure 4.18, which shows four species and five traits, each of which exists in two alternative states. Let us suppose that we do not know which states are primitive and which are derived. Because each of the two states (0 and 1) could be either primitive or derived, and because there are five characters, there are 2^5 or 32 possibilities for which states are primitive and which are derived.

Let us simplify by focusing on four possibilities, each corresponding to the case in which one of the observed species shows the primitive state for all characters. The four resulting cladograms with their character-state changes are shown in Figure 4.18b. These look quite different from one another, but in fact they have some features in common. In all four cases (as well as the 28 other cases not shown here), tracing the path between A and B, or between C and D, involves two character transitions on the clado-gram; tracing between A or B on the one hand and C or D on the other hand involves three transitions.

These common features can be summarized in an unpolarized or **unrooted network,** in which the characters that must be changed to transform one set of character states to another are indicated, and in which character change can be traced in either direction. Regardless of character polarity, there will always be one node between A and B, one between C and D, and two between A or B on the one hand and C or D on the other hand.

In practice, computer programs generally proceed by constructing unrooted networks because, with fewer unrooted than rooted networks, the computational load is substantially reduced. The network is then converted to a **rooted** cladogram, typically by choosing a set of taxa as the ingroup and one or more taxa as outgroups, which polarizes the characters.

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the shape of the shell, and the modified musculature—constitute a correlated character complex rather than three independent characters.

There is as yet no general solution to the problems of character correlation and weighting, and this represents an important area for future work. One should ideally avoid treating characters as independent if they are known to be strongly correlated, but the presence of character complexes is not always so clear as in the case of epibyssate bivalves.

Accuracy of Estimated Phylogenies

An obvious question will have occurred to the reader by now: How well in fact does the most parsimonious cladogram estimate the true evolutionary relationships

that it attempts to portray? We have little reason to think that evolution acts parsimoniously (minimizing convergence and reversal), so why should we expect parsimonious cladograms to be accurate?

Two general approaches have been taken to assess the accuracy of parsimony and other phylogenetic methods. First, methods have been tested in groups that have been studied for so long and in such detail that we think we know something about their evolutionary relationships, as with parts of the tetrapod cladogram (Figure 4.10). Second, they have been tested with artificial evolutionary trees, generated by computer simulation of evolution, controlled laboratory breeding, and other procedures.

Although the detailed results of such investigations are beyond the scope of this book, one generalization
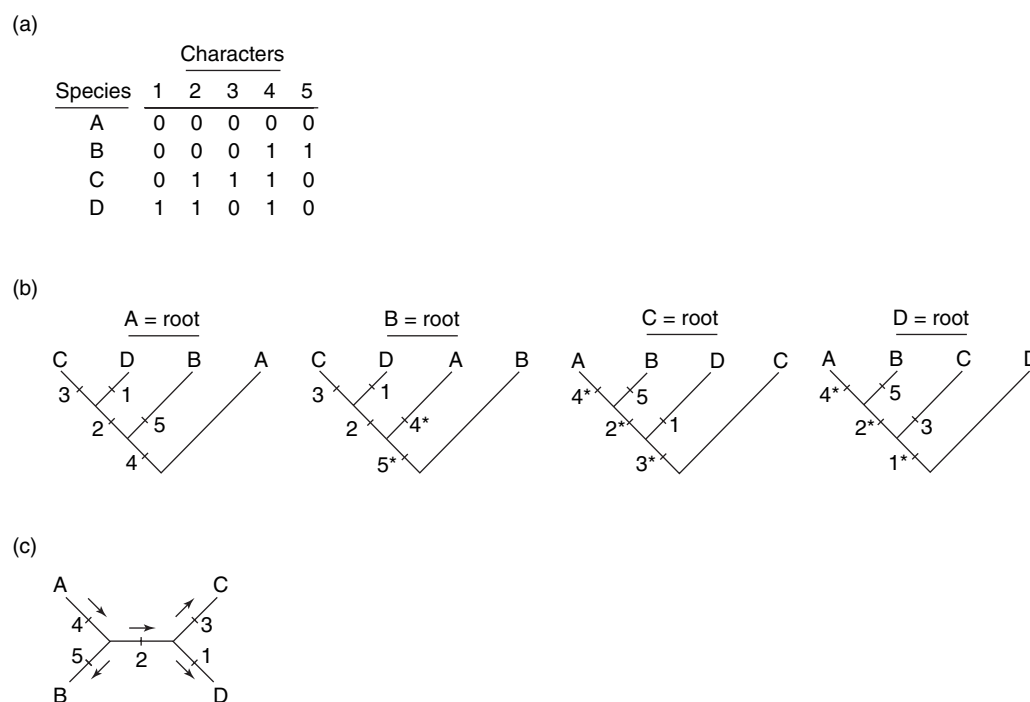
(a)

	Characters				
Species	1	2	3	4	5
A	0	0	0	0	0
B	0	0	0	1	1
C	0	1	1	1	0
D	1	1	0	1	0

(b)

(c)

FIGURE 4.18 Example of cladogram construction when character polarity is unknown. (a) Character data. (b) Four possible cladograms, each corresponding to the assumption that one of the sampled species shows the primitive state in all characters. For example, if B is assumed primitive, then 0 is the primitive state for characters 1, 2, and 3, while 1 is the primitive state for characters 4 and 5. Each character number on the cladogram denotes a character transition. Those marked with an asterisk indicate transition from state 1 to state 0; others indicate transition from state 0 to state 1. (c) Unrooted network showing the topology of relationships among the four species. Arrows indicate the direction of change from state 0 to 1. Regardless of the polarity of characters, A and B are separated by two transitions (4 and 5); C and D are separated by two transitions (1 and 3); AB is separated from CD by one transition (2); and either of the pair AB is separated from either of the pair CD by three transitions (4 or 5; 2; and 1 or 3).

that emerges is that parsimony seems to work well when the rate of evolution is relatively low (so that the chances of reversal or convergence are low), and when characters evolve independently (as required by the practice of equal weighting). These conditions make obvious sense, because they should lead evolution to act parsimoniously. That parsimony works well when these conditions hold does not mean that it absolutely requires them, however. In fact, the set of evolutionary assumptions underlying parsimony has not yet been fully specified (Sober, 2004).

Cladistic parsimony will also tend to be more accurate to the extent that all lineages have the same rate of character evolution. The violation of this condition is of special interest in paleontology and evolutionary biology. If lineages differ substantially in evolutionary rate [SEE SECTION 7.1], and if the characters studied have a limited number of alternative states, then there will be a tendency for those lineages that evolve more rapidly to group together even if they are not most closely related. Although the issue is complex, it can be seen intuitively that the artificial grouping of distantly related lineages reflects their increased probability of attaining the derived character state independently, because of the high rate of evolution in those lineages to the exclusion of others. This problem is generally referred to as **long-branch attraction** (the length of a branch referring to the amount of evolutionary change along that branch of the evolutionary tree).

Other Approaches

The approach to phylogenetic inference we have described here, cladistic parsimony, is by far the most commonly used method when the data at hand are morphological, as is nearly always the case in paleontology. Many other methods exist, however. What most of them have in common is that they evaluate numerous alternative cladograms or trees and find the set of these that optimize some criterion—just as parsimony minimizes the number of evolutionary steps implied by a cladogram.

One such optimality criterion that has received much attention is the probability that a hypothesized cladogram, *under an assumed model of evolution*, would yield the observed character data. In this context, the corresponding probability is proportional to what is known as the **likelihood;** the cladogram that maximizes this quantity is considered the **maximum-likelihood estimate** of the phylogeny (see Box 4.7). The evolutionary model

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Box 4.7

MAXIMUM-LIKELIHOOD ESTIMATION OF PHYLOGENY

Figure 4.19 illustrates the likelihood approach with a very simple example involving three hypothetical species. In actual cases with more realistic assumptions, the steps will differ from those shown here, but the ultimate criterion for choosing among cladograms is the same. Figure 4.19a shows the data matrix, and Figure 4.19b gives the three alternative cladograms whose likelihoods are to be evaluated.

The following assumptions are made for the sake of this example: (1) The characters are polarized, so that 0 is the primitive state for each. The basal node, marked X on the cladograms, is primitive in all characters. (2) For each of the cladograms there are four opportunities for character change, corresponding in three instances to the transition from a node (common ancestor) to a terminal taxon, and in one instance to the transition between the two nodes, X and Y. For each of these four opportunities, the probability of change from 0 to 1 is assumed to be the same. This probability is denoted P. The probability that character state 0 will not change to state 1, given that is has the opportunity to do so, is equal to $1 - P$. (3) There is no reversal from the derived state to the primitive state (from 1 to 0).

The distributions of character states among the three species are given by $0\ 0\ 1$ for character 1, by $0\ 1\ 1$ for character 2, and by $1\ 0\ 0$ for character 3. The essence of the analysis is to compute the probability of attaining these character distributions under each alternative phylogenetic hypothesis. Consider character 1, and look first at cladogram I. To be present in the derived state only in species C requires that the character

changed once, from node X to C, and that it failed to change three times, from X to Y, from Y to A, and from Y to B. The net probability is thus $P(1 - P)^3$ (see Figure 4.19c).

Similar reasoning for the other two cladograms shows that in each case the probability of attaining the character distribution $0\ 0\ 1$ is equal to $P(1 - P)^3$. Because the probability of observing the distribution $0\ 0\ 1$ is the same regardless of the cladogram, it is not possible to distinguish the likelihood of the three cladograms on the basis of this character. The same is true of character 3, with distribution $1\ 0\ 0$, which also has a probability of $P(1 - P)^3$ for all three cladograms. These results should not be surprising because the characters in question are present as unique rather than shared novelties.

Let us turn now to character 2, which has distribution $0\ 1\ 1$. In cladogram I, the derived state must have evolved twice independently, once from X to C and once from Y to B. Keeping in mind that we have assumed no reversal from 1 to 0, character 2 must also have failed to evolve from X to Y and from Y to A. Thus, the overall probability of distribution $0\ 1\ 1$, given cladogram I, is $P^2(1 - P)^2$. The same result holds for cladogram II.

In cladogram III, there are two possible ways that the character distribution may have resulted. First, the derived state may have evolved twice independently, from Y to B and from Y to C, and failed to evolve twice, from X to Y and from X to A. The corresponding probability is $P^2(1 - P)^2$. Second, the derived state may have evolved once, from X to Y, after

generally contains elements such as the probabilities of transition between alternative character states and the number of different evolutionary rates—ranging from the simplest model in which all lineages and characters evolve at the same rate to more complex models in which each lineage is characterized by a unique rate.

Likelihood methods have several potential advantages. In contrast to cladistic parsimony, the underlying model of evolution is made explicit and can therefore be assessed directly. Moreover, the statistical foundations

of likelihood analysis are well developed, and the relative strength of support for alternative cladograms can be evaluated rigorously. Perhaps most important, likelihood may yield more accurate cladograms than parsimony in certain cases, notably that of unequal rates, where long-branch attraction is relevant. Unfortunately for paleontologists, likelihood analysis has been developed mainly for DNA sequence data, where models of evolution are easiest to define. It is nonetheless applicable in principle to morphological data, and the

which it was passed on to both B and C, and failed to evolve once, from X to A. The corresponding probability is $P(1 - P)$. Thus, the overall probability of character distribution 0 1 1, given cladogram III, is equal to $P^2(1 - P)^2 + P(1 - P)$. This is obviously greater than the probability of the same character distribution given either cladogram I or II, namely,

$P^2(1 - P)^2$. Because the probability of the observed data is highest with cladogram III, this cladogram is considered the maximum-likelihood estimate. In light of the assumptions that were made for this exercise, it should come as no surprise that this is the same cladogram that would be preferred by cladistic parsimony. In general, however, this need not be the case.
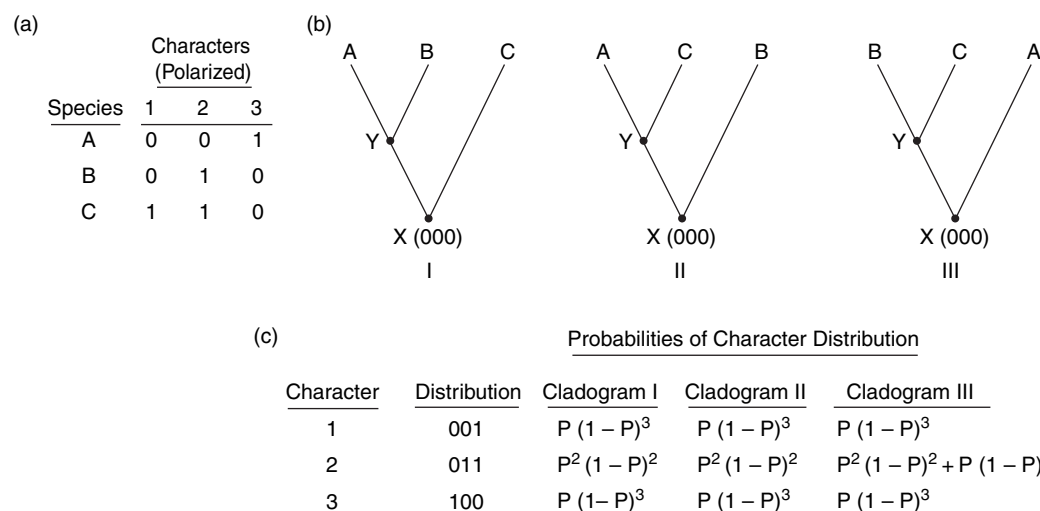

(a)

Species	Characters (Polarized)		
	1	2	3
A	0	0	1
B	0	1	0
C	1	1	0

(c) Probabilities of Character Distribution

Character	Distribution	Cladogram I	Cladogram II	Cladogram III
1	001	$P(1-P)^3$	$P(1-P)^3$	$P(1-P)^3$
2	011	$P^2(1-P)^2$	$P^2(1-P)^2$	$P^2(1-P)^2 + P(1-P)$
3	100	$P(1-P)^3$	$P(1-P)^3$	$P(1-P)^3$

FIGURE 4.19 **Example of cladogram assessment by the principle of likelihood, which evaluates the probability of observing the given data if the postulated cladogram is correct.** (a) Character matrix. (b) Three postulated cladograms. The probability that any character will evolve from 0 to 1 along a segment of the cladogram is P; the probability that it will not do so is $1-P$. The relevant cladogram segments are between one node and the other (X to Y) or between a node and a terminal species. It is assumed that characters do not revert from 1 to 0. (c) Characters 1 and 3 yield equal likelihoods for all cladograms and so are not informative. Character 2 yields the highest likelihood for cladogram III, which is therefore preferred.

FIGURE 4.20 One way of incorporating stratigraphic position after a cladogram is established. (a) Character data: 0 is primitive and 1 is derived. (b) The most parsimonious cladogram for these data. (c) Stratigraphic position of sampled species. (d) Postulated tree with A ancestral to BC. Because A is autapomorphic in character 3, this tree requires secondary loss of this character. (e) Postulated tree with A and BC sharing unsampled common ancestor. No character reversal is required.
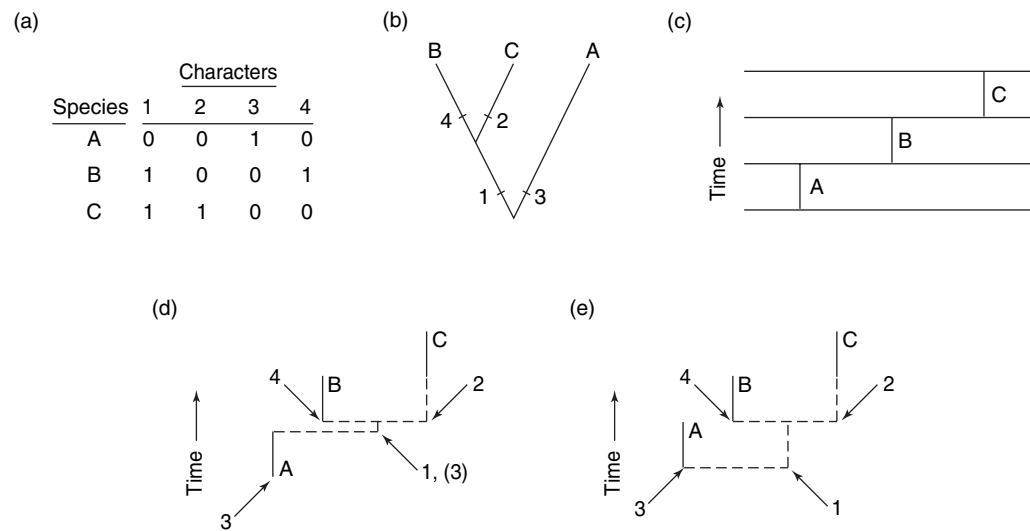
continued refinement of likelihood methods is expected to be an important development for systematic biology and paleontology.

The Temporal Dimension in Genealogy

We have so far focused on the reconstruction of genealogical relationships in the form of a cladogram, but for many paleontological questions it is important to have evolutionary trees. For all practical purposes, the construction of evolutionary trees is equivalent to the incorporation of stratigraphic or temporal data [SEE SECTION 6.1] into the process of phylogenetic inference.

There are two principal ways of incorporating stratigraphic data into phylogenetic analysis. The first uses morphological data to reconstruct cladistic relationships and only subsequently adds stratigraphic position to form evolutionary trees. The second incorporates data on stratigraphic occurrences as a fundamental part of the reconstruction of evolutionary relationships. Here we present just one variant of each general approach.

Consider the character data, cladogram, and temporal occurrences for three hypothetical lineage segments (Figure 4.20). The character data clearly support the grouping A(BC); B and C share the derived state of character 1 to the exclusion of A. The fact that A occurs stratigraphically below B and C might seem to suggest that it is ancestral to these two (Figure 4.20d). However, A possesses a novelty that should be present in B and C if A were ancestral. To maintain that A is ancestral requires the loss in the (BC) lineage of that trait unique to A. This is less parsimonious than supposing that A and

(BC) share a common ancestor (Figure 4.20e), with A's novelty evolving after the divergence between the lineage leading to A and that leading to (BC).

A contrasting case occurs when A is fully primitive relative to B and C and it contains no novelties of its own (Figure 4.21). Here it is plausible and parsimonious to reconstruct A as ancestral to (BC). Thus, the general guideline is that a taxon that is stratigraphically lower and fully plesiomorphic relative to its cladistic sister taxon may be interpreted as potentially ancestral to it. An actual example of this procedure is shown in Box 4.8.
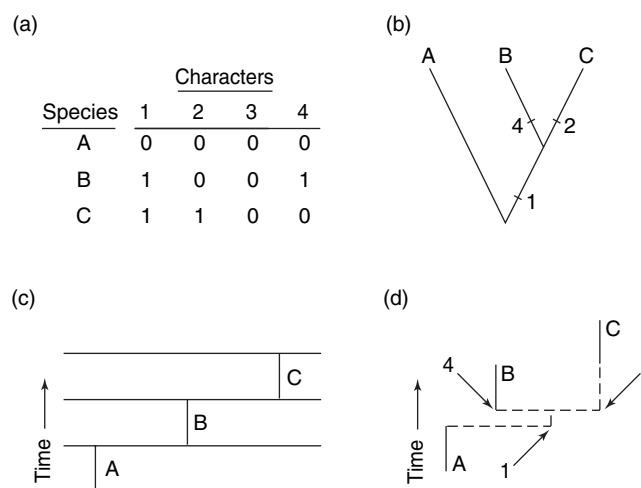

FIGURE 4.21 One way of incorporating stratigraphic position when a species is fully plesiomorphic. (a) Character data: 0 is primitive and 1 is derived. (b) The most parsimonious cladogram for these data. (c) Stratigraphic position of sampled species. (d) Evolutionary tree with A ancestral to BC. Because A has no apomorphies, postulating that it is ancestral to BC requires no evolutionary reversals.

Many paleontologists have recognized that stratigraphic data have the potential to do more than distinguish between the terminal and ancestral placement of a taxon after the cladogram is derived from morphological data. One method that has been developed to incorporate stratigraphic position into the reconstruction of

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Box 4.8

TREE CONSTRUCTION IN A SAMPLE OF ARBACIOID ECHINOIDS

Construction of the evolutionary tree in this example follows the principles illustrated in Figures 4.20 and 4.21. Figure 4.22a shows the cladogram resulting from parsimony analysis of character data. Names of outgroups are in boldface. The asterisk indicates an extinct genus, the (−) indicates a genus that has no apomorphic character states relative to its sister taxon, and the (+) indicates one or more apomorphic states. The (?) indicates that it is uncertain which of the sister genera *Coelopleurus* and *Murravechinus* is primitive relative to the other—an uncertainty that stems from the presence of both primitive and derived states in *Coelopleurus*.

Figure 4.22b shows the stratigraphic ranges of sampled genera and the evolutionary tree consistent with the cladogram. In constructing this tree, the stratigraphically earlier member of a pair of sister taxa is

placed in an ancestral position if it lacks apomorphic states, as in Figure 4.21. An example is that of *Acropeltis*, which gives rise to *Goniopygus*. By contrast, the stratigraphically earlier member of a pair of sister taxa is placed in a terminal position if it has apomorphic states. An example is that of *Glyphopneustes*, which does not give rise to *Arbia*. The placement of *Coelopleurus* as ancestral to *Murravechinus* is based on stratigraphic position. The cladistic relationships of *Hemicidaris*, *Hypodiadema*, and *Gymnocidaris* are based on a number of equally parsimonious cladograms that, unlike Figure 4.22a, place *Hemicidaris* and *Hypodiadema* as sister taxa.
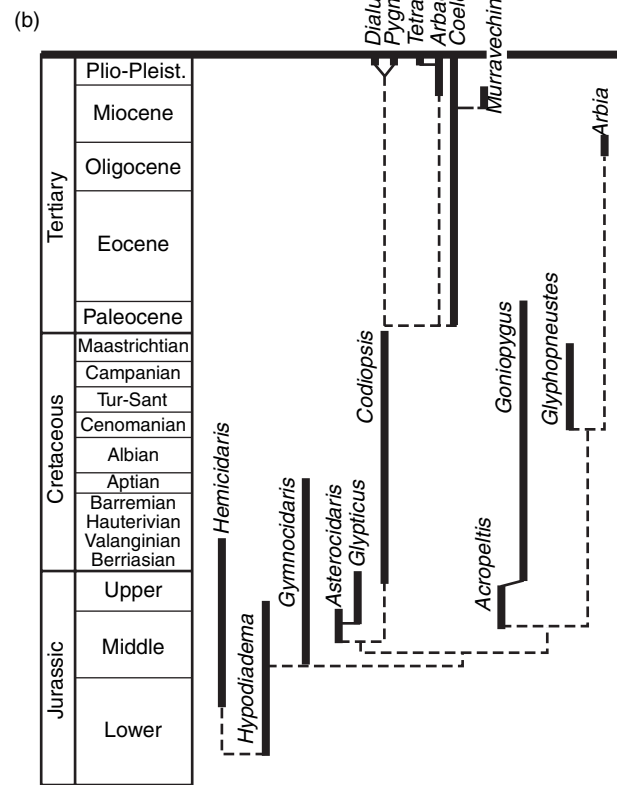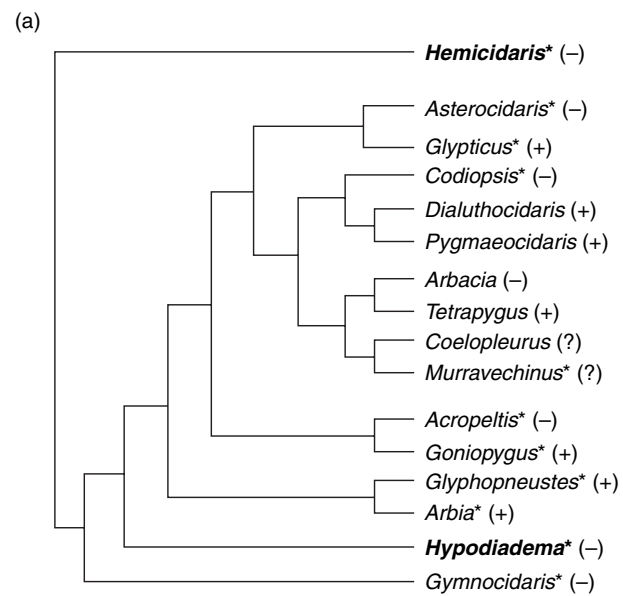

FIGURE 4.22 **Tree construction in a sample of arbacioid echinoids.** (a) Cladogram. (b) Stratigraphic ranges of sampled genera and evolutionary tree. Observed ranges are shown by thick vertical bars. Dashed lines show inferred evolutionary relationships. *(a: Courtesy of Andrew B. Smith; b: From Smith, 1994)*

the cladogram itself is **stratocladistics.** The essence of stratocladistics is to treat morphological and stratigraphic data as logically equivalent classes of information. This means that the same criterion—parsimony—is used to evaluate the consistency between a postulated evolutionary tree and observed data, whether the data are morphological or stratigraphic (Box 4.9).

4.3 CLASSIFICATION

One of the main purposes of a classification, whether of species or of inanimate objects, is to summarize and retrieve information efficiently. This aids the memory

and also facilitates communication. The ideal classification of species summarizes information on morphological attributes while at the same time reflecting what is known about evolutionary relationships. For example, if a paleontologist reports a new fossil arthropod, nearly any scientist will immediately infer that the organism is characterized by those traits typical of the phylum Arthropoda, such as a chitinous exoskeleton and jointed limbs. If the paleontologist goes on to report that the specimen is in the class Trilobita, the order Asaphida, and the superfamily Asaphoidea, then the typical trilobite features—such as a three-lobed body, fused tail region or pygidium, and two-branched

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Box 4.9

STRATOCLADISTICS

We have already seen what parsimony means for morphological data. Figure 4.23 illustrates the concept of stratigraphic parsimony. An evolutionary tree under evaluation is considered unparsimonious to the extent that it postulates the existence of unobserved lineages at a time and place where we would expect to observe them if they had in fact existed—that is, in deposits suitable for their preservation. The echinoid tree of Figure 4.22, for example, implies many unobserved lineages (dashed vertical lines). The suitability of preservation can be judged on the basis of facies characteristics or the presence of taphonomic control taxa [SEE SECTION 1.1].

The morphological data in Figure 4.23a support the grouping A(BC) (Figure 4.23c). One possible evolutionary tree that is consistent with this grouping (Figure 4.23d) has A ancestral to C, which in turn is ancestral to B. This tree requires the existence of C, or a lineage leading to it, throughout two stratigraphic intervals in which it was not in fact sampled. Each such unsampled lineage segment is said to contribute a unit of **stratigraphic parsimony debt.** Because the number of evolutionary steps on this tree is the minimal number that there can be for two derived character states, there is no **morphological parsimony debt.**

Another possible tree (Figure 4.23e) has A giving rise to B, persisting for some time, and giving rise to C as well. This tree is not consistent morphologically with the grouping A(BC) because the tree implies that A is as

close to B as it is to C. The tree involves one unit of stratigraphic debt, because there is a postulated lineage segment leading from A to C that is not preserved, and one unit of morphological debt, because the derived state in character 3 must have evolved twice. If stratigraphic and morphological debt are given equal weight, this tree is overall just as parsimonious as the first, even though it is less parsimonious morphologically.

A third tree, of many that could be postulated, has A ancestral to B, which in turn is ancestral to C (Figure 4.23f). This tree requires no unsampled lineage segments, so there is no stratigraphic debt. It does, however, imply one unit of morphological debt because it requires the secondary loss in C of the derived state of character 2. Of the trees considered here, this one involves the lowest combined morphological and stratigraphic parsimony debt. It is therefore preferred by the method of stratocladistics.

In the hypothetical example of Figure 4.23, we assumed that units of morphological and stratigraphic debt carry the same weight. Nevertheless, just as cladistics allows for the differential weighting of characters if some are believed to be more or less susceptible to convergent evolution, stratocladistics can give different weight to certain unobserved lineage segments if there is evidence that the fossil record is more or less complete in the corresponding stratigraphic intervals. In other words, if we know that the record is fairly complete, we impose a large penalty for pos-

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limbs—will come to mind for nearly any paleontologist or biologist. The typical asaphide features, such as the specialized larva, will also be suggested to the trilobite specialist.

Thus, the classification allows detailed information on anatomy to be conveyed with just a few words. In the trilobite example, the phylum, class, and order are also clades. Therefore, the placement of the specimen in this classification allows one to infer that it is genealogically more closely related to other arthropods, such as crustaceans, than it is to molluscs; that it is closer to other trilobites, such as phacopides, than it is to crustaceans; and that it is closer to other asaphide trilobites, such as trinucleoids, than it is to phacopides.

Nature of Higher Categories

The classification of species into higher categories that has developed over the years, deriving from the standardization of Carl Linnaeus (1758), is a nested hierarchy. The kingdom contains one or more phyla, the phylum contains one or more classes, and so on down to species within genera. At the same time, it is a nonoverlapping hierarchy. A species belongs to only one genus, a genus to only one family, and so on. The most commonly used

tulating lineages that are not actually observed. And if we know that geologically appropriate deposits are absent or scarce, we forgive the stratigraphic debt implied by missing lineage segments because it is quite plausible that they existed but simply were not preserved. Stratocladistics can also give less weight to stratigraphic data as a whole than to morphological data if the taphonomic controls are not strong.
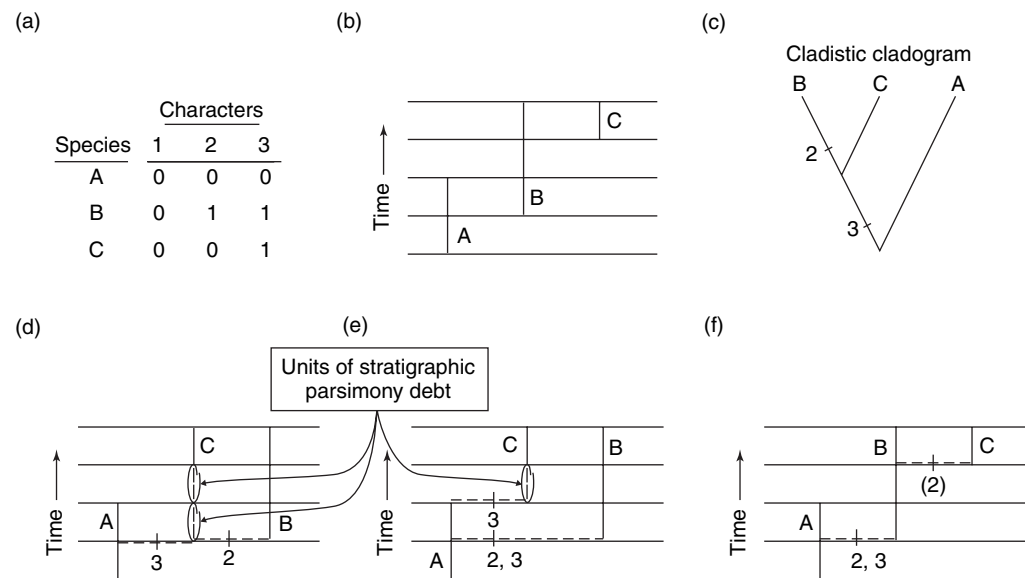

FIGURE 4.23 Stratocladistic analysis of hypothetical data. (a) Character data: 0 is primitive and 1 is derived. (b) Stratigraphic ranges of sampled taxa. (c) The most parsimonious cladogram corresponding to character data. (d–f) Three possible evolutionary trees corresponding to character data and stratigraphic ranges. Tree (d) requires neither character reversal nor repeated evolution of any character, but it does require that the lineage leading to species C existed for 2 time units without being sampled. Tree (e) requires that character 3 evolved twice and that the lineage leading to species C went for 1 time unit without being sampled. Tree (f) requires that character 2 reverted to the primitive state, but it does not require any unsampled lineages. Tree (d) is preferred by cladistics, while tree (f) is preferred by stratocladistics.

taxonomic categories between the kingdom and species levels are the phylum (or division) class, order, family, and genus, although it is customary, especially in groups with many species, to use numerous intermediate levels such as the subphylum, subclass, superorder, suborder, superfamily, subfamily, and subgenus.

The *International Code of Zoological Nomenclature* includes rules and recommendations for formation of higher categories. The rules are approximately parallel to those for species. It is generally assumed that all genera can be assigned to families, orders, and so on, although allowance is given for the possibility that the evolutionary affinities of a genus may be unknown. In such a case, the genus may be defined in isolation or in **open nomenclature** ("incertae sedis"). The type concept also extends to the definition of higher categories. When a new genus is proposed, a **type species** designation must accompany the original description. The type species thus becomes the name bearer for the genus. Similarly, a family must have a **type genus,** and so on.

A grouping of species may be **monophyletic,** meaning that it consists of a common ancestor and all its descendants (Figure 4.24)—in other words, a clade, as defined earlier. It is a discrete branch of an evolutionary tree. Familiar examples of monophyletic higher taxa include the phylum **CHORDATA,** the class Mammalia, and the order Primates. Similar in some ways to monophyletic groupings are those that are **paraphyletic,** consisting of a common ancestor and some but not all of its descendants. A paraphyletic group is, broadly speaking, ancestral to one or more groups, meaning that the lineage giving rise to the descendant group is part of the paraphyletic group.
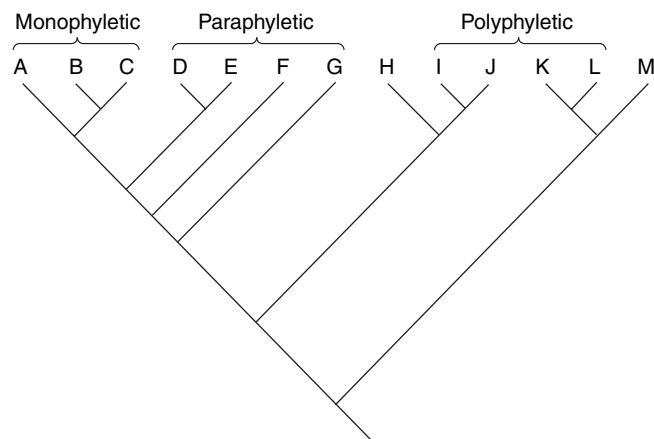

FIGURE 4.24 Cladogram showing examples of monophyletic, paraphyletic, and polyphyletic groups.

Referring back to the tetrapod cladogram of Figure 4.10, the groups traditionally referred to as amphibians and reptiles are paraphyletic. Roughly speaking, amphibians are tetrapods that are not amniotes, and reptiles are amniotes that are neither birds nor mammals. A **polyphyletic** grouping of organisms is one whose members do not derive from a single common ancestor within the group. Winged vertebrates (including pterosaurs, birds, and bats) would be an example of a polyphyletic group. In light of the dual goals of a classification—summarizing evolutionary relationships as well as morphological traits—polyphyletic groups are generally undesirable, and we will not discuss them further.

This threefold terminology is the most widely used, and we will adopt it for the sake of discussion. Some systematists use the term *monophyletic* to incorporate both paraphyletic and monophyletic groups as defined here, referring to the latter as **holophyletic** or **strictly monophyletic.**

Inclusiveness and Rank

In erecting a category above the species level, two quite distinct decisions need to be made: Which lower-level taxa will be included within it, and which level or **rank** (genus, family, order, and so on) will be designated for it? The answer to these questions in any given case is subject to considerable influence of judgment and experience of practicing systematists, and such issues are not legislated by the Code. Unlike phylogenetic inference, to which algorithmic approaches have been applied quite successfully, attempts to erect classifications by strict rules have generally failed.

Given an accurate evolutionary tree, there can be no question as to whether two species are on the same branch or not. This, however, does not answer the question of whether they should be classified together in a given higher taxon. A classic example of this problem is seen in alternative classifications of humans and closely related primates. A large body of genetic data supports the union of humans and *Pan* (chimpanzee and bonobo) as most closely related among living primates, to the exclusion of gorillas and other great apes (Figure 4.25). There have nonetheless been conflicting classifications of this group, some emphasizing the apparent morphological divergence of humans and placing them in a distinct family (with *Pan* and *Gorilla* in a separate, paraphyletic family). A generally accepted approach today unites *Homo*, extinct humans, *Pan*, *Gorilla*, and *Pongo* into a single, monophyletic family, Hominidae.
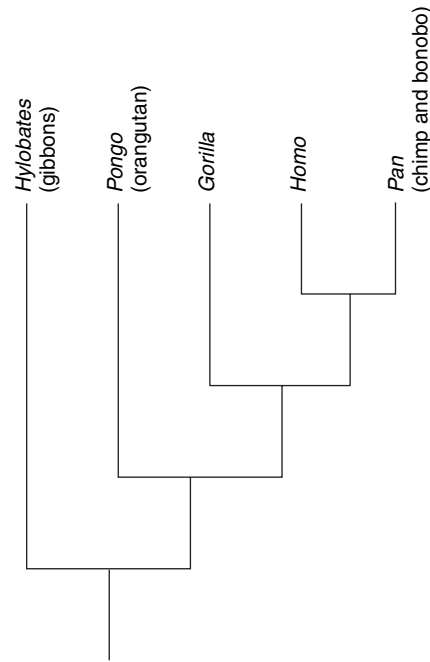
FIGURE 4.25 Cladogram showing relationships among living humans and great apes. This represents a composite of numerous studies, based on both morphological data and DNA sequences. *(After Purvis, 1995)*

Just as the inclusiveness of a higher taxon cannot be determined by rigid rules, the rank is also subject to considerable judgment even if taxonomic composition is not at issue. Should humans and chimpanzees be classified as different species within the same genus, or as different genera within the same family? The answer is largely subjective. Many systematists maintain the ideal that rank should be proportional to the magnitude of morphological differences among taxa. Species are separated by small differences, genera by larger differences, and so on.

Although morphological difference is undoubtedly important in assigning rank, other criteria have been used as well. Perhaps most common is evolutionary success, or the accumulation of diversity over time. It has often been said that if birds had not survived past the Jurassic, the class Aves would not have been erected, and *Archaeopteryx* and its relatives would instead have been classified as perhaps a single family within theropod dinosaurs (Figure 4.10).

Higher rank has also been applied to primitive, paraphyletic groups from which arose one or more groups that are given high rank. For example, within the echinoderm subphylum **BLASTOZOA,** the primitive group referred to as **EOCRINOIDS** evidently gave rise to numerous class-level taxa (Figure 4.26). Many of these—for instance, the Blastoidea and Coronata—are clearly monophyletic. In most classifications, the paraphyletic eocrinoids are also formally named as a class.

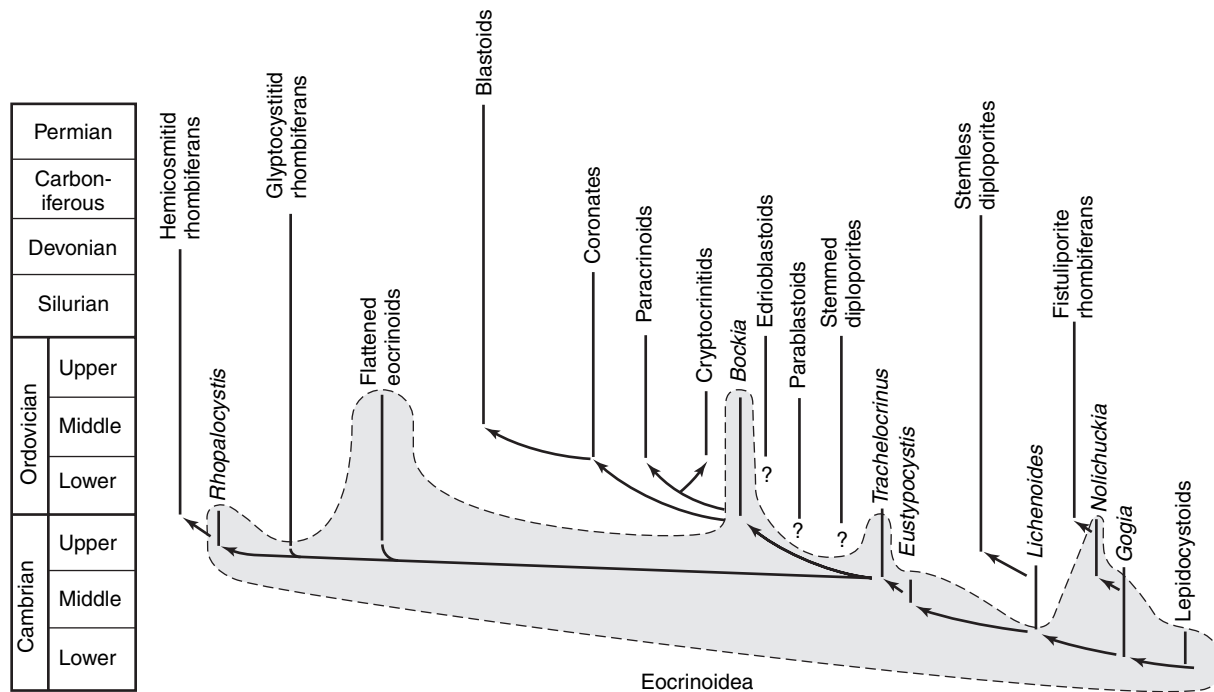If a particular higher rank is used for some members of a phylum or class, it may be used for all or most

FIGURE 4.26 One postulated evolutionary tree of blastozoan echinoderms. The paraphyletic class Eocrinoidea is indicated by the shading. *(From Paul & Smith, 1984)*

members, even though this is not mandatory. For example, the subclass rank is customarily used in classifying crinoids. The Middle Cambrian *Echmatocrinus brachiatus*, initially described in 1973, is thought by some workers to be a crinoid, but its affinities with other crinoids are uncertain. It has been assigned to a **monotypic** genus, family, order, and subclass. Similar to this practice is that of assigning identical rank to sister clades.

Box 4.10

PARAPHYLETIC TAXA IN PALEONTOLOGY

There have been several arguments against the use of paraphyletic taxa:

• Drawing the line between a paraphyletic group and a monophyletic group derived from it is often seen as arbitrary, as this line could be drawn at many different places on the evolutionary tree equally well. Of course, the resulting monophyletic group is no less arbitrary in this regard than is the paraphyletic group. Phylogenetic taxonomy only dictates that groups be defined on the basis of shared novelties; it does not give a formula for which particular novelties to use and therefore which set of species to include in a given taxon. The only completely nonarbitrary system would be to define every single monophyletic grouping as a higher taxon (Figure 4.27). This, however, would involve such a proliferation of taxonomic names as to make the resulting classification, in many cases, cumbersome and inconvenient.

• Paraphyletic taxa are defined in part by the traits they lack rather than the traits they possess. Referring back to Figure 4.26, the eocrinoids possess the feeding structures called *brachioles* that characterize blastozoan echinoderms, but they are distinguished from other groups of blastozoans mainly in lacking novel traits that evolved in other lineages. From the perspective of phylogenetic systematics, the retention of primitive characters is of no particular significance, and there is little that unites eocrinoids; they are simply the residue left after recognition and extraction of many monophyletic groups.

• The first and last appearances in time of genera and families, many of which are paraphyletic, are often used to document patterns of taxonomic origination and extinction in the fossil record [SEE SECTIONS 7.2, 8.5, and 8.6]. Times of elevated turnover of higher taxa are commonly thought to mark elevated turnover of species as well. Some workers have questioned this, however, suggesting that paraphyletic taxa tend to distort underlying species-level patterns.

This last problem is illustrated in Figure 4.28. Part (a) shows a hypothetical evolutionary tree with a concentration of species extinctions at the end of stratigraphic interval 5. Figure 4.28b presents one
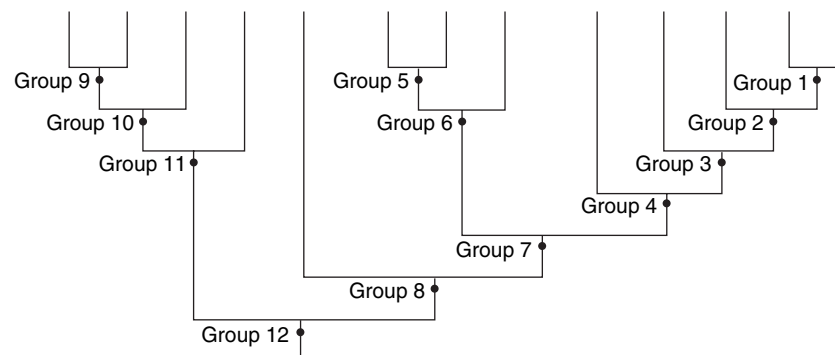

FIGURE 4.27 Hypothetical cladogram showing many nested, monophyletic groups. A worker constructing a cladistic classification must decide which of these groups to describe as formal higher taxa, and what taxonomic rank to apply to them.

This has an obvious logic, but, like other approaches, it leaves open the question of what the rank should be.

One question about taxonomic inclusiveness has assumed much importance in paleontology: Is it good practice to erect paraphyletic higher taxa? An essential component of what has been called **phylogenetic classification** is that only monophyletic higher taxa should be permitted. For more detail, see Box 4.10.
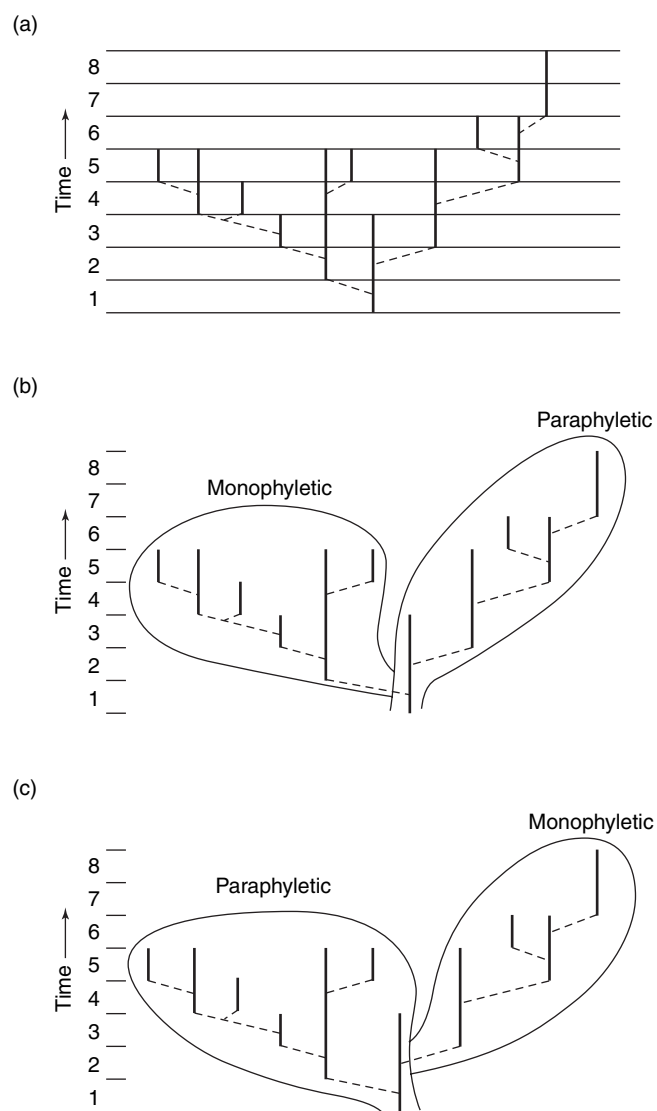

(a)

(b)

Monophyletic

Paraphyletic

(c)

Paraphyletic

Monophyletic

FIGURE 4.28 Species extinction and higher taxonomic extinction. (a) Hypothetical evolutionary tree divided into higher taxa in two different ways (b, c), each of which yields one monophyletic group and one paraphyletic group. Many species become extinct in interval 5. In part (b), this event is marked by the last appearance of the monophyletic taxon; in part (c), it is marked by the last appearance of the paraphyletic taxon. *(After Fisher, 1991)*

possible way of dividing this tree into two higher taxa, one monophyletic and one paraphyletic. According to this classification, the last appearance of the paraphyletic taxon does not coincide with the concentration of species extinctions, but that of the monophyletic taxon does. Thus, it would be misleading to use the extinction of the paraphyletic taxon as a surrogate for an underlying species extinction event. There is nothing inherent in paraphyletic taxa, however that requires them to be misleading in this way. According to an alternative classification (Figure 4.28c), it is in fact the paraphyletic taxon whose last appearance marks the extinction of numerous species, whereas the last appearance of the monophyletic taxon coincides with little in the way of species-level turnover.

In point of fact, it is as yet unknown whether the situation in Figure 4.28b or Figure 4.28c is more common, and actual examples of each have been documented. In other words, it is not known just how serious this particular concern about paraphyletic taxa will turn out to be.

Paraphyletic taxa can be quite useful in reflecting important morphological, functional, and ecological distinctions. Birds are phylogenetically nested within dinosaurs, but maintaining a separate, paraphyletic taxon for dinosaurs is nonetheless thought by many to summarize substantial anatomical and physiological distinctions.

From the paleontological standpoint, perhaps the most compelling argument in favor of permitting paraphyletic higher taxa is that evolutionary trees reconstructed from the fossil record incorporate not only sister-taxon relationships but also ancestor–descendant relationships. Every ancestor is by its very nature paraphyletic. In groups with a sparse fossil record, ancestor–descendant pairs are relatively unlikely to be discovered; most sampled taxa will be terminal, and a classification free of paraphyletic groups

4.4 CONCLUDING REMARKS

We have discussed phylogenetic inference as if it were mainly a matter of how to process data. In fact, the most crucial step in phylogenetics is careful morphological analysis, with a detailed understanding of ontogeny, sources of variation, correlations among traits that would affect the assumption of character independence, and prior knowledge of evolutionary transitions. Experience has shown that those paleontologists who have produced the most compelling and believable phylogenies are not necessarily those with the best computational skills, but rather those with the detailed knowledge of a group of organisms that is needed for sound morphological analysis.

Even when two paleontologists agree completely on the subject of evolutionary relationships, they may disagree on the ideal manner in which to summarize these relationships, as well as other information, in a classification. It is our feeling that the information and convenience sacrificed by a classification system that allows only monophyletic taxa outweighs the advantages of such a system (see Box 4.10). Nevertheless, a number of paleontologists have adopted fully phylogenetic classifications of the groups they study. We expect to see extensive developments in the area of phylogenetic classification, as evolutionary

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Box 4.10 (continued)

may be feasible. In those groups that make up the majority of the fossil record, however, it is quite likely that ancestor–descendant pairs are preserved and that paraphyletic taxa will therefore be a practical necessity.

One proposed system for circumventing the conflict between phylogenetic classification and paleontological data involves dispensing with the need to place every species in a taxon of every rank from genus up through phylum. This system distinguishes the **crown group,** the monophyletic group containing living species and extinct species that nest among them, from the **stem group,** the paraphyletic remainder that consists only of extinct species (Figure 4.29). The stem group is not formally named as a higher taxon, and monophyletic groups within the stem group are named as **plesions.** These plesions may be given an optional rank, but they are not nested within successively higher taxa.

Table 4.4 shows such a classification for the echinoids of Figure 4.22a. Note that informal taxonomic categories are used (such as "Unnamed subfamily 1" and "Group 1") and that the genus *Hemicidaris* is interpreted not to be monophyletic but is divided
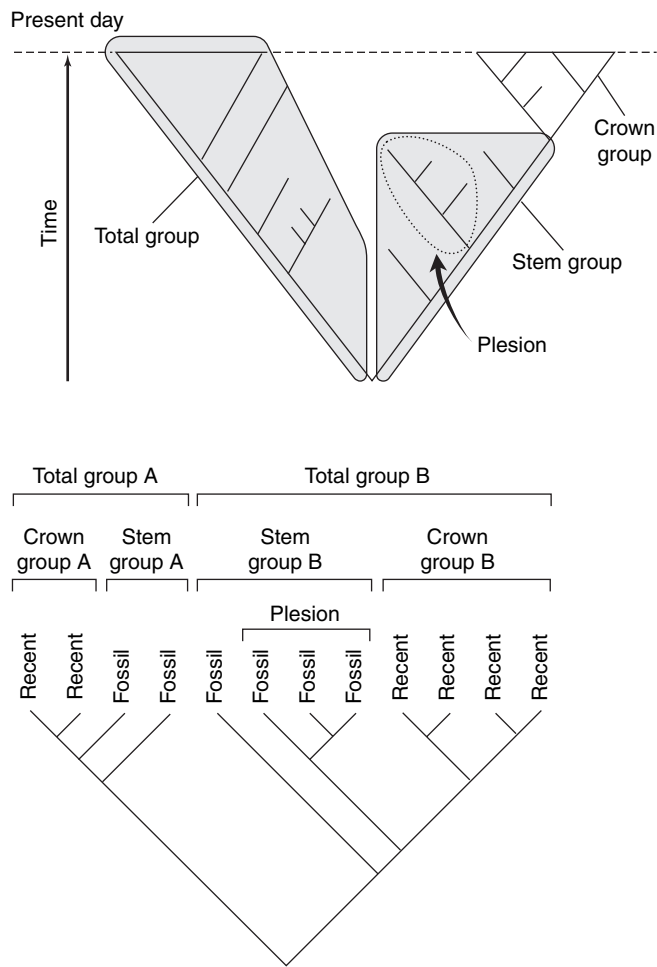

FIGURE 4.29 Illustration of crown groups, stem groups, and plesions. (a) Hypothetical evolutionary tree. (b) Cladogram. Each part of the figure shows one plesion of many that could be identified. *(From Smith, 1994)*

relationships are progressively resolved and as electronic storage and retrieval of classification schemes make the dense nesting of exclusively monophyletic groups and the crown–stem–plesion system (Box 4.10) easier to apply.

One such development that is currently under way is the writing of a **phylogenetic code** for species nomenclature. One version of this code would dispense with assigning species to genera and other higher taxa unless these higher taxa are demonstrably monophyletic. This would be a radical departure from the traditional, binomial nomenclature that has evolved since the time of Linnaeus. Related to this development is the consideration of an alternative to the bio-

logical species concept [SEE SECTION 3.3]. The proposed **phylogenetic species concept** defines a species as having a shared evolutionary history independent of other species. This history should lead the populations within a species, just like the species within a clade, to be united by synapomorphies. Operationally, this concept therefore considers a species to be "the smallest aggregation of populations . . . diagnosable by a unique combination of character states" (Nixon & Wheeler, 1991). To what extent a formal phylogenetic code of nomenclature will prove useful to working biologists and paleontologists, and will therefore be adopted, remains to be seen.

between two subfamilies. Note also that three plesions (*Hypodiadema*, *Gymnocidaris*, and *Codiopsis*) may be ancestral, and thus paraphyletic, according to the evolutionary tree of Figure 4.22b. Unnamed subfamily 2 and the sister genus pair *Dialuthocidaris* + *Pygmaeocidaris* constitute the two crown groups in this classification.

Although the crown–stem–plesion system enables phylogenetic systematics to cope with paleontologi-

cal data to some extent, it is not applicable to the many fossil groups, such as trilobites, that are completely extinct. Moreover, by not mandating the ranking of extinct taxa, it may lead to classifications that fall short in their potential for information storage and retrieval, especially for groups such as brachiopods, cephalopods, and crinoids, which contain vastly more extinct than living forms.

TABLE 4.4

Classification of the Echinoids of Figure 4.22, Illustrating the Use of Plesions

Order Arbacioida Gregory	Unnamed plesion 2
Plesion (Genus) *Hypodiadema* Desor	Genus *Glypticus* Agassiz
Plesion (Family) Hemicidaridae Wright	Genus *Asterocidaris* Cotteau
Subfamily Hemicidarinae Smith and Wright	Family Arbaciidae Gray
Genus *Hemicidaris* Agassiz (in part)	Unnamed subfamily 1
Subfamily Pseudocidarinae Smith and Wright	Plesion (Genus) *Codiopsis* Agassiz
Hemicidaris termieri Lambert	Genus *Dialuthocidaris* Agassiz
Plesion (Genus) *Gymnocidaris* (Agassiz)	Genus *Pygmaeocidaris* Doderlein
Unnamed plesion 1	Unnamed subfamily 2
Family Acropeltidae Lambert	Group 1
Genus *Acropeltis* Agassiz	Genus *Arbacia* Gray
Genus *Goniopygus* Agassiz	Genus *Tetrapygus* Agassiz
Family Glyphopneustidae Smith and Wright	Group 2
Genus *Glyphopneustes* Pomel	Genus *Coelopleurus* Agassiz
Genus *Arbia* Cooke	Genus *Murravechinus* Philip

SOURCE: Smith (1994)

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