



5-1-2002

Artificial Keys to the Genera of Living Stalked Crinoids (Echinodermata)


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Recommended Citation

Roux, Michel, Charles G. Messing, and Nadia Ameziane. "Artificial keys to the genera of living stalked crinoids (Echinodermata)." *Bulletin of Marine Science* 70, no. 3 (2002): 799-830.

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ARTIFICIAL KEYS TO THE GENERA OF LIVING STALKED CRINOIDS (ECHINODERMATA)

Michel Roux, Charles G. Messing and Nadia Améziane

ABSTRACT

Two practical, illustrated, dichotomous keys to the 29 genera of living stalked crinoids are provided: one for entire animals and one for stalk ossicles and fragments. These are accompanied by (1) an overview of taxonomically important morphology, and (2) an alphabetical list by family and genus of the ~95 nominal living species and their distribution by region. This is the first compilation of such data for all living stalked crinoids since Carpenter (1884) recognized 27 species in six genera in his monograph based on the H.M.S. CHALLENGER Expedition collection.

Modern stalked crinoids are often viewed as the archetypal ‘living fossils’, a few relict remnants of a once glorious Paleozoic past, clinging to precarious existence in remote deep-sea habitats (Russell-Hunter, 1969; Thurman, 1975; McConnaughey and Zottoli, 1983; Thurman and Weber, 1984). As with many simplifications, however, the view is more false than true (Roux, 1987).

It is true that stalked crinoids no longer exist in shallow water. However, *Metacrinus rotundus* occurs on the outer shelf in as little as 100 m off Japan (Oji, 1986), and the majority of extant species occur at bathyal (<1000 m) rather than abyssal depths. A few records of several species (e.g., *Saracrinus angulatus*, *Metacrinus musorstomae*, *Democrinus* spp.) exist from as little as 55–70 m, but these are dredging depths that require verification (A. H. Clark, 1912; Meyer et al., 1978; Roux 1981).

Yes, stalked crinoids are no longer as abundant as they once were. Unstalked crinoids, the comatulids or feather stars, are far more abundant and diverse in modern seas (Meyer and Macurda, 1977). They first appeared in the Triassic, but the modern fauna derives from a major adaptive radiation since the Late Miocene (Roux, 1987). About 540 nominal species are recognized (Messing, 1997). Further, no living populations currently generate the vast crinoidal limestones produced during the late Paleozoic and Mesozoic (Ausich, 1997; David and Roux, 2000a). Yet, about 95 modern stalked species are known in 29 genera (see Améziane and Roux, 1997). Only about five times as many genera existed during the entire Early Mississippian Period, the acme of crinoid diversity (Keim, 1978), and modern species richness exceeds that of any individual Mesozoic horizon. Some extant stalked taxa, particularly in the tropics (e.g., Messing et al., 1990) and north-eastern Atlantic (Conan et al., 1981), occur in substantial meadows and may represent the dominant macrobenthic organisms in their communities. Here, they may contribute up to 52% of the coarse fraction to local sediments (being overwhelmed chiefly by the skeletons of pelagic foraminiferans and gastropods, both unknown before mid-Cretaceous) (Llewellyn and Messing, 1991, 1994).

Finally, it is true that many living stalked crinoid taxa have familial roots in the Mesozoic and have changed little in overall morphology since that time. The oldest documented roots are for the family Pentacrinidae (including Isocrinidae, see below), which definitely dates to the latest Triassic (Keim, 1978; Simms, 1988) and probably to the Permian (Webster and Jell, 1999), and remains highly diversified today. Several Meso-

zoic families survive with only single 'living fossil' species (i.e., the Liassic Eudesicrinidae represented by *Proeudesicrinus lifouensis*, the Late Jurassic to Early Cretaceous Hemicrinidae by *Gymnocrinus richeri*, and the Jurassic Millericrinidae by *Proisocrinus ruberrimus*) (Amézière-Cominardi et al., 1990). The family Bathycrinidae dates to the Late Jurassic (Bourseau et al., 1991) and Holopodidae to Mid-Cretaceous, perhaps to Late Jurassic (Amézière et al., 1999). However, many modern non-crinoid marine taxa also first appeared during the Mesozoic as products of multiple adaptive radiations. Indeed, much of the modern stalked crinoid fauna is rooted in a Late Cretaceous to Recent adaptive radiation (Roux, 1987).

We offer these dichotomous artificial keys to the extant genera of stalked crinoids for several reasons. The literature is extremely diffuse. Diagnoses of all living genera have not been available in a single published source since Carpenter (1884) recognized six genera in his monograph based on the CHALLENGER Expedition (1872–76) collections. A. H. Clark, who published over one hundred papers on modern crinoid taxonomy between 1907 and 1950, added nine genera, but never consolidated the information into a single paper. Rasmussen and Sieverts-Doreck (1978) diagnosed 20 of the 26 genera that they considered as having Recent representatives. More recent work, especially by French scientists, has significantly increased the number of taxa, especially of unusual ones such as *Gymnocrinus*, *Caledonicrinus* and *Guillecrinus* (e.g., Roux, 1985; Bourseau et al., 1987, 1991; Amézière-Cominardi et al., 1990; Mironov and Sorokina, 1998a,b). This research has also begun to force a reassessment of the relationships among crinoid groups set forth in the *Treatise on Invertebrate Paleontology* (Rasmussen and Sieverts-Doreck, 1978). For example, Simms (1988) offered the first analysis of relationships among post-Paleozoic crinoids using cladistic techniques, while Amézière-Cominardi and Roux (1994) pointed out some problems raised by such phylogenetic reconstructions, basing their discussion on ontogeny and evidence of frequent pedomorphic processes.

We recognize that phylogenetic reconstructions should include extinct forms. However, because this key is intended to be a practical guide for marine scientists, we have omitted fossil taxa. Also, several fossil taxa require re-examination before some taxonomic knots can be untied. Unfortunately, such questions spill over into the extant fauna because the relationships between several living species and genera based on extinct species remain to be clarified. Our taxonomic placement of some species is, therefore, tentative.

Please note also that the stalked crinoids do not constitute a monophyletic or even formal taxonomic group. They merely represent all those species that do not belong to the unstalked comatulids, or feather stars. A stalk does confer a certain functional similarity on those species possessing one by implying a combination of sessility and elevated feeding apparatus. However, two genera traditionally treated broadly as stalked (*Holopus* and *Cyathidium*) lack a stalk (Amézière et al., 1999), members of the Pentacrinidae are not sessile (Messing et al., 1988), and many comatulids attain a functionally stalked condition via extremely long cirri or by attaching to elevated perches (e.g., alcyonarians, antipatharians and stalked crinoids) (Meyer and Macurda, 1980). We omit comatulids from the following key except to note how they may be distinguished as a group. They are the subjects of a far more extensive taxonomic literature. Messing (1997) reviews comatulid morphology and current literature, and provides a key to extant families.

Most of the specimens illustrated herein are housed in the Muséum national d'Histoire naturelle, Paris (MNHN). MNHN catalogue numbers preceded by EcPs refer to dry speci-

mens; those preceded by EcPh refer to those preserved in ethanol. Other sources include the National Museum of Natural History (Smithsonian Institution) (USNM); Natural History Museum, London (BMNH); Bishop Museum, Oahu, Hawaii; National Institute of Water and Atmosphere (NIWA), Wellington, New Zealand, and the crinoid collection at Nova Southeastern University's Oceanographic Center (NSU). Additional abbreviations are as follows: JSL: Deep Submergence Vehicle Johnson Sea Link; WHOI: Woods Hole Oceanographic Institute. All illustrations are by CGM. Scanning electron micrographs were taken by MR and NA at the Interuniversity Center for Scanning Electron Microscopy (C.I.M.E.) at the Universities of Paris VI and VII.

CRINOID MORPHOLOGY

GENERAL FORM AND ORIENTATION

A typical crinoid consists of a segmented stalk that supports a small central body, or theca, from which five usually branched rays, or arms, radiate (Fig. 1A). The crown refers to the theca and rays together (i.e., the entire animal exclusive of the stalk). The theca consists of a calyx that encloses the central visceral mass and an overlying, sometimes-calcified membrane, or tegmen, that bears mouth, anus and hydropores (openings leading into the water vascular system) and defines the oral surface. Structures associated with the opposite surface are aboral. In those groups in which the calyx is reduced, the viscera rest on the bases of the rays. Five ambulacra radiate from the central mouth across the tegmen onto the rays and their branches. Each consists of a ciliated food groove lined with fingerlike, food-collecting podia (extensions of the water vascular system) and bordered by epidermal folds called lappets. An extensive mesodermal endoskeleton, consisting chiefly of articulated series of calcareous pieces called ossicles, essentially determines morphology and forms the basis of much of crinoid taxonomy. An axial canal carrying extensions of coelomic and nervous systems passes through each ossicle. As in other echinoderms, the fine structure of the ossicles forms a fenestrated meshwork (stereom). Because the skeleton is highly repetitive, symbols for different skeletal parts greatly condense taxonomic descriptions.

In orienting parts of a crinoid, distal describes a direction or position away from the central aboral/oral axis, toward the tip of a structure (e.g., ray, arm, cirrus or pinnule) or toward the anchoring end of the stalk. Proximal is toward the aboral/oral axis, the base of a structure (=basal), or the upper end of the stalk. Abambulacral refers to a direction away from or opposite the surface bearing the food groove (=aboral). Adambulacral is toward the surface bearing the food groove. Adoral refers to a position toward the mouth or mouth-bearing surface.

We refer the reader to Breimer (1978) for a more detailed treatment of crinoid morphology, Carpenter (1884), A. H. Clark (1915, 1921) and Ubaghs (1953) for historical perspectives, and Macurda and Meyer (1975), Roux (1975, 1977, 1980, 1981), Macurda et al. (1978), Macurda and Roux (1981) and Donovan and Pawson (1994) for analyses of crinoid skeletal microstructure.

STALK

The stalk is the series of ossicles that arises from the center of the aboral surface of the theca and supports the body above and fixes it to the substrate (Fig. 1A,B). The central, supportive member is the column, composed of columnals, which are circular, pentago-

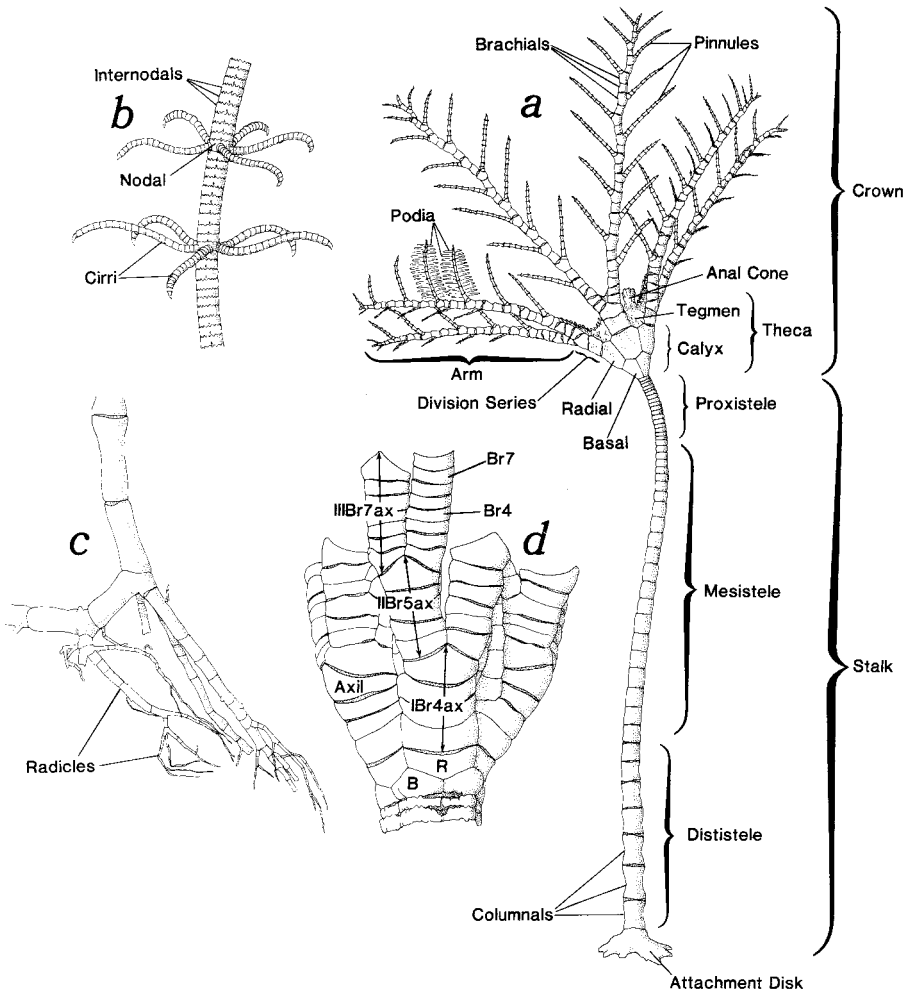


Figure 1. A. Schematic illustration of a generalized crinoid with a xenomorphic stalk; three of five rays are shown. B. Portion of a heteromorphic stalk with cirri. C. Portion of a terminal stalk radix. D. Proximal portion of a crown showing bases of three rays and abbreviations for primi-, secondi- and tertibrachial series, and individual brachials of the undivided arm. R = radial ossicle; B = basal ossicle.

nal, stellate or elliptic (rarely hexagonal) in cross section and range from thin and discoid to tall and cylindrical. They may also be barrel-, spool- or hourglass-shaped. Columns range from a few centimeters to over a meter in length and may consist of over 350 columnals. Homeomorphic columnals consist of similar columnals that may change gradually along the length of the column. Heteromorphic columns consist of different kinds of columnals distributed along most or the entire column (e.g., nodals alternating with series of internodals, see below) (Fig. 1B). In xenomorphic columns, the proximal, middle and distal sections of the stalk (also called proxistele, mesistele and dististele, respectively) each consist of different kinds of columnals (Fig. 1A). Each of these stalk sections

may be either homeomorphic or heteromorphic. The various kinds of articulations that link columnals are discussed below.

In genera with a reduced column (e.g., *Gymnocrinus*, Fig. 3A), it is unclear if the remaining columnals derive from multiple fused ossicles and, if so, how many (Bourseau et al., 1991). Certainly, proximal columnals partly fuse to each other in some genera and the proximal end of the column fuses completely with the calyx in others. Two extant genera, *Cyathidium* (Fig. 3C) and *Holopus* (Fig. 3D), appear to have suppressed the column completely and attach via the expanded aboral base of the calyx (Améziane et al., 1999). Both are usually treated together with more typical stalked crinoids. By contrast, the comatulids, which shed all but the uppermost columnal following a stalked postlarval pentacrinoid stage, are distinguished as unstalked crinoids. As noted above, they are not treated herein.

Many stalked crinoids (e.g., *Hyocrinus*, *Phrynocrinus*) cement to hard substrates via an expanded terminal columnal, an attachment disk, that may encrust irregular substrates (Fig. 1A). All extant crinoids (perhaps excepting *Holopus*, *Proeudesicrinus* and *Cyathidium*) probably attach in this manner at least as postlarvae and, perhaps, juveniles. Alternatively, the column may develop accessory anchoring structures. In some (e.g., *Metacrinus*, *Teliocrinus*), modified columnals called nodals that occur at intervals along the stalk each bear a whorl of five cirri: unbranched, usually hook-like or prehensile appendages composed of ossicles called cirrals (Fig. 1B). The terminal cirral is often hooked and claw-like (Conan et al., 1981). The series of non-cirrus-bearing internodal columnals between successive nodals is called an internode (Figs. 1B, 5C, G). Most species anchor either via the cirri arising from the terminal nodal or those along a distal portion of stalk that lies recumbent along the substrate. These crinoids can release their cirri from the substrate, either partly in order to elevate or lower the crown, or completely in order to crawl with their arms (Messing et al., 1988). In other genera (e.g., *Democrinus*, *Bathycrinus*), one or more distal columnals bear slender branched or unbranched radicles that together form a root-like radix for anchoring in unconsolidated substrates (Fig. 1C). Radicles have been called radicular cirri, but, unlike true cirri, they do not arise from well-defined sockets in columnals modified as nodals. Following Breimer (1978), we omit the use of the term radicular cirri.

CALYX, RAYS AND ARMS

The calyx of extant crinoids consists of one, two or three circlets of rigidly attached ossicles immediately above the stalk (Fig. 1A). It is often used synonymously with aboral (or dorsal) cup. However, the latter is better treated as a functional entity that may incorporate proximal columnals and/or tegmental plates in addition to calyx circlets. Five radials compose the uppermost calyx circlet; each is associated with one of the five internal radial canals of the water vascular system that arise from the circumoral ring canal (Fig. 1A, D). The term is also used as an adjective: structures associated with the extrapolated central axis of these ossicles have a radial orientation. By contrast, three to five basals lie between the radials and the stalk and alternate with the radials. That is, the center of a basal ossicle usually lines up with the border between adjacent radials; their orientation, and that of any similarly placed structure, is interradian. Distinct suture lines may demarcate both basals and radials, or they may be variously fused. A third series of calyx ossicles, the radially oriented infrabasals, occur in some extant taxa between the basals and the stalk, but only as reduced internal elements. Calyx ossicles vary from thin-walled

plates that form a hollow cup that encloses the viscera (e.g., Fig. 10), to small ossicles together no wider than the top of the column (Figs. 7A, 8A, C). Morphology, proportions and extent of fusion of calyx ossicles are often critical diagnostic features at subordinal, familial and generic levels.

Arm (or brachium) and ray are two terms that refer to the usually branched series of ossicles and associated soft tissues that radiate from the central body. A ray begins with a radial ossicle whereas an arm begins with the first ossicle following a radial. Use of one versus the other has derived largely from morphology. In crinoids with reduced calices and with radials similar to the following ossicles (e.g., *Metacrinus*, Fig. 4D), the term ray is often used. In this context, arm refers to the series of ossicles following the most distal branching point. In crinoids with a well-developed calyx (e.g., *Hyocrinus*, Fig. 10G), the term arm refers to the entire distinct, often much narrower, series of ossicles following the large radial.

Whether arm or ray is used, brachial ossicles follow the radials. Brachitaxes (or division series) are series of brachials between branch points, either following a radial and including the first ossicle at which the ray branches (axillary or axil), or following an axil and including the next (Fig. 1A, D). Each axil bears two articular faces distally and may thus bear two additional brachitaxes, two unbranched arms, or one of each. Interior and exterior arms, brachitaxes or associated structures are those closest to and furthest from, respectively, the extrapolated axis of the preceding branching series. The first three brachitaxes, beginning immediately following the radials, are often specified as primibrachial, secundibrachial and tertibrachial series, composed of primi-, secundi- and tertibrach ossicles, respectively. Branching patterns are often diagnostic at generic and, sometimes, family levels (Fig. 1D).

Pinnules are the small, segmented, unbranched appendages that arise on alternating sides of successive brachials, give the arms their characteristic featherlike appearance and are the primary site of food-collection (Fig. 1A). They are composed of ossicles called pinnulars.

Symbols.—To condense descriptions, crinoid researchers designate ossicles and series of ossicles by a substantial variety of abbreviations. To avoid burdening the reader with unnecessary nomenclature, we outline only basic usage and some variations that appear in the current literature.

In one system, widely used for pentacrinoids, each brachial is indicated by Br followed by an Arabic number indicating its place in the sequence from proximal to distal. Ossicles in brachitaxes are preceded by a Roman numeral beginning with the most proximal, e.g., II Br₃ is the third ossicle in the second brachitaxis; Br₅ is the fifth ossicle of an undivided arm. An appended ax (for axil) indicates an entire brachitaxis, e.g., III Br₆ax is the third brachitaxis composed of 6 ossicles, the last of which is an axil (Fig. 1D).

In another system, used for comatulids, each successive brachial is indicated by br followed by an Arabic number subscript. Ossicles in brachitaxes are again preceded by a Roman numeral (e.g., II br₃ for the third ossicle in the second brachitaxis; br₅ for the fifth brachial of the undivided arm). Entire brachitaxes are designated by a Roman numeral, Br and an Arabic number (e.g., III Br₆).

Unlike comatulids, most stalked crinoids exhibit little differentiation among oral (proximal), genital (gonad-bearing) and distal pinnules. As a result, specific pinnules rarely require identification. Where necessary, however, individual pinnules are indicated by P followed by a subscript Arabic number or lower case letter for successive exterior or interior pinnules, respectively (e.g., P₁, P₂, P_a).

ARTICULATIONS

Successive ossicles articulate via ligaments or combinations of muscles and ligaments that anchor in depressions (fossae) on the articular faces (or facets). Stalked crinoids appear to have four basic articulations: synostosis, symplexy, syzygy and synarthry (Fig. 2). The latter is often highly modified during development or with growth into several secondary articular forms that may converge on the first three.

A synostosis is effectively rigid, with apposed ossicle faces flat or shallowly concave, and united by relatively few, short ligament fibers. It appears externally as a straight or gently curved suture and may occur between columnals (Fig. 2B), brachials or calyx ossicles.

Syzygies are rigid brachial articulations in which alternating radiating ridges and depressions or grooves on the two joint faces appose each other rather than interlock; the external suture resembles a perforated line. They are widespread among comatulids but occur in stalked crinoids only in the arms of *Guillecrinus* and *Vityazicrinus* (Fig. 2H).

In a symplexy, found only between columnals, ridges (culminae) on one joint face interlock with corresponding grooves (crenellae) on the apposed face; the articulation appears externally as a wavy suture. In adult pentacrinitids (Fig. 2A), the grooves and ridges (an adjacent pair of which are treated together as a crenula) border five petal-like regions around the central lumen of the axial canal. In adult hyocrinids (Fig. 2C), radially arranged crenulae occur in a zone called the crenularium.

The basic synarthry (Fig. 2D) bears a central fulcral ridge that separates a pair of semi-circular fossae, each of which houses a large ligament bundle. This articulation links most columnals in juvenile stalks and adult xenomorphic stalks (e.g., *Bathycrinus*, *Phrynocrinus*). In external view, the ends of ossicles joined by synarthry converge where the fulcral ridges reach the edge of each articular face. Fulcral ridges on the opposite articular faces of a columnal orient at different angles to each other, permitting the stalk to bend in multiple directions.

In the basic synarthry between brachials, the fulcral ridge orients through the oral/aboral (=ambulacral/abambulacral) axis of the articular face. In most synarthrial articulations between successive brachials, called muscular articulations, the fulcral ridge orients diagonally or transversely, and one pair each of interarticular ligaments and muscle bundles insert on the ambulacral side of the fulcral ridge (Fig. 2G). Frequently (e.g., in pentacrinitids and comatulids), stereom differs between fossae anchoring ligaments (galleried stereom) and those anchoring muscles (labyrinthic stereom with or without needle-like projections) (Macurda et al., 1978). In a few stalked crinoids (e.g., Hyocrinidae and Holopodidae) stereom anchoring ligaments and muscles are indistinguishable, because galleried stereom is absent from ligamentary fossae (Roux and Pawson, 1999; Amézière et al., 1999).

Sometimes, in all kinds of articulations, a general depression of one ossicle facet corresponds to a complementary relief on the other. Such a feature is called a symmorphy (Figs. 2E,F).

Frequently, a juvenile articulation may be modified during development so that the adult facet shows a composite pattern derived from different ontogenetic stages. In *Porphyrocrinus* or *Calamocrinus*, for example, the central zone of a columnal facet exhibits a juvenile morphology (synarthry or symplexy), while the surrounding area is a synostosis or syzygy. Such morphologies reveal the transformation of a flexible juvenile articulation into an adult rigid articulation. In the heteromorphic pentacrinitid stalk, the distal joint of a nodal ossicle is a symplexy in the proximal part of the stalk (the juvenile columnal stage) and transforms into a synostosis distally (the mature columnal stage),

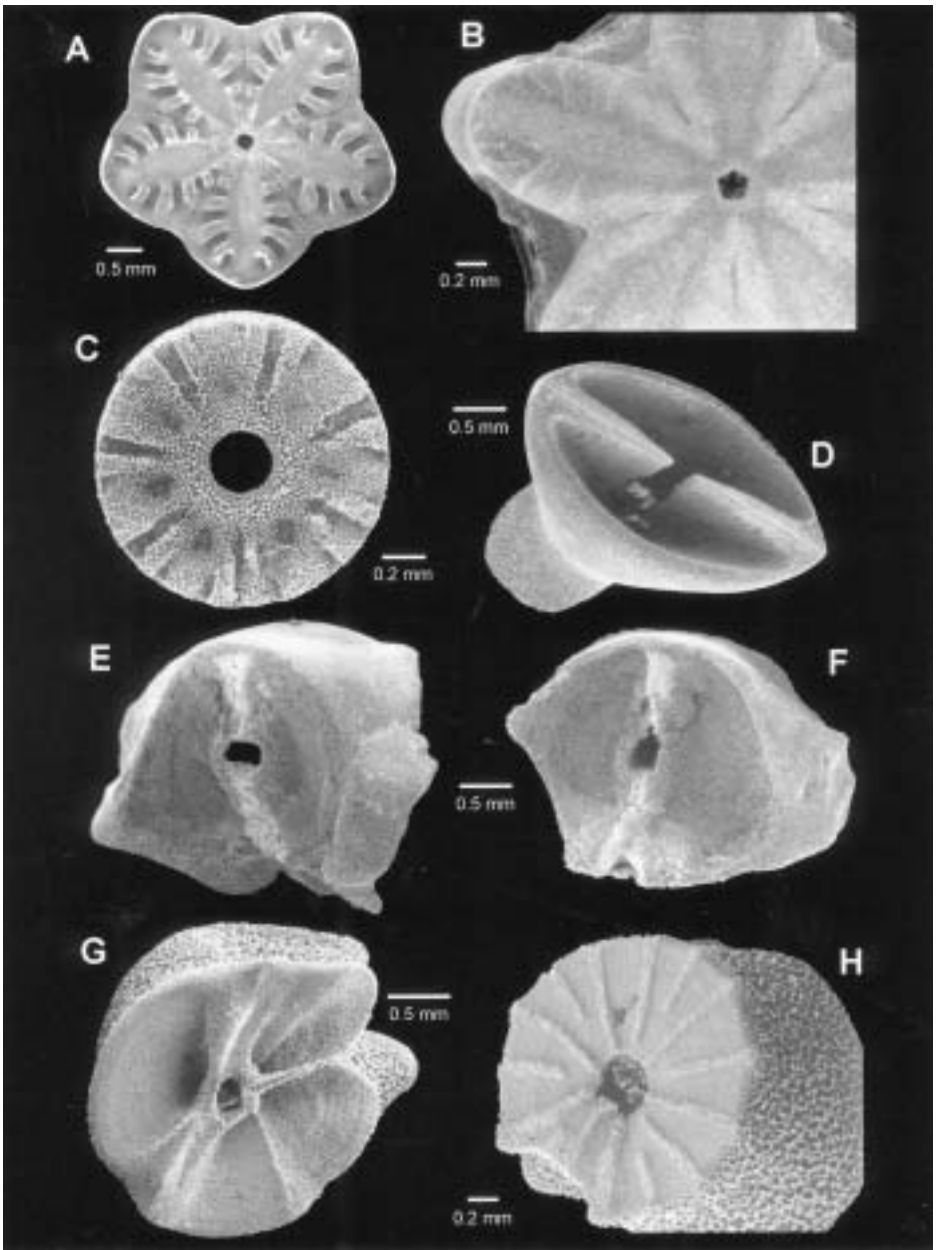


Figure 2. Main types of articulations in stalked crinoids. A, B, E, F. *Teliocrinus springeri*. A. Pentalobate symplexy of internodal in heteromorphic stalk. B. Pentalobate cryptosymplexy (secondary synostosis) of distal facet of nodal in heteromorphic stalk. E, F. Transverse synarthry with symmophy in proximal arm. C. *Ptilocrinus pinnatus*, multiradiate symplexy in homeomorphic stalk. D. *Porphyrocrinus incrassatus*, synarthry in distal portion of xenomorphic stalk. G–H. *Guillecrinus neocaledonicus*. G. Muscular synarthry in arm. H. Non-muscular syzygy in arm.

where autotomy becomes possible (Fig. 2B). This transformation develops via deposition of a fine synostosomal stereom over the juvenile symplexial facet, producing a flat rigid articulation called a cryptosymplexy. In arm articulations, a proximal synostosis may perhaps develop from a juvenile synarthry (as a cryptosynarthry), but such an ontogenetic transformation has yet to be demonstrated.

In a few species (i.e., *Hypalocrinus naresianus* or *Neocrinus blakei*), a juvenile flexible, non-muscular synarthry between proximal brachials transforms with growth into a symmorphial synarthry, in which a strong ridge on the distal articular facet lodges in a corresponding valley in the facet of the proximal ossicle. In external aboral view, the articulation appears V- or U-shaped (Fig. 5B, arrow a). In a transverse synarthry, the ridge and valley run from side to side across the arm; the suture line is convex distally in aboral view and forms a deep V on each side of the ossicle pair (Figs. 2E,F, 5B, arrow b). Both ossicles may bear weak crenellations along their aboral margins. In large adult specimens, such an articulation becomes rigid.

Note that the proximal brachial of a pair joined by any exclusively ligamentary articulation never bears a pinnule.

Symbols.—In the literature, a plus sign (+) indicates a non-muscular articulation between two brachials [e.g., IIBr4(3+4) is a second brachitaxis of four ossicles with the third and fourth joined by non-muscular articulation]. Unfortunately, three different non-muscular articulations exist: syzygy, synostosis and transverse synarthry. In comatulid arms, non-muscular articulations with flat facets are generally syzygies, while, in stalked crinoids, synostoses are most frequent. Until a consistent system is developed, we omit all use of abbreviations for articulations.

TEGMEN

As noted above, the tegmen, the upper surface of the theca, covers the visceral mass. It may be flat (Fig. 6B) or inflated (Fig. 10E,J) and bears the central mouth, five radiating ambulacra and the anus, located off-center in one of five interambulacral areas at the apex of a small anal cone (Fig. 1A). In many taxa, either with reduced calyx ossicles or with an enlarged visceral mass, the tegmen is elevated, sometimes to the level of the eighth brachial in unbranched forms, or even beyond the second brachitaxis in branched forms. In such cases, the proximal portions of the rays with the tegmen extending proximally between them form a functional theca above the radials.

The tegmen often bears a variety of small calcareous plates or scales that may be isolated or form a generally flexible pavement. In some cases (e.g., *Caledonicrinus*, *Proisocrinus*), such plates form a solid pavement over the oral surface and between adjacent rays. The ambulacra, though sometimes lined with one or more rows of protective plates, are usually open grooves. In a few cyrtocrinid taxa (e.g., *Holopus*, *Cyathidium*, *Hyocrinus*), large, triangular, interradially-oriented oral plates can close over the mouth. In *Gymnocrinus* (Fig. 3A), however, the proximal brachials completely roof the grooves.

THE KEYS

We offer two dichotomous keys for identifying stalked crinoids. Because many species are known from one or a few specimens, and numerous taxonomic questions remain, the keys extend at best to the generic level, except for monospecific genera.

The first treats entire animals. Because dredges and trawls often retrieve crownless or fragmentary stalks, we provide an additional key for stalks, which may often be identifi-

able only to family. This latter key omits crinoids attached directly by the base of the theca (i.e., *Holopus*, *Cyathidium*) and those that lose the stalk following a stalked postlarval stage (i.e., comatulids). Both keys are artificial in that they are based on practical, easily recognizable morphological features. They do not necessarily reflect phylogenetic relationships, which remain to be worked out in detail.

Several separate keys have previously been published for different modern stalked crinoid taxa and are useful for additional details or for discussions. The main references are: A. H. Clark (1923) and Roux (1981) for Pentacrinitidae; Gislén (1938) and Roux (1977) for Bathyocrinidae, Bourgueticrinidae and Phrynocrinidae, and Roux (1980) and Mironov and Sorokina (1998a,b) for Hyocrinidae.

KEY 1. THE GENERA OF LIVING STALKED CRINOIDS

- 1a. Segmented stalk absent (e.g., Figs. 3C,D) 2
- 1b. Segmented stalk present (e.g., Figs. 1A,3A,6,8) 4
- 2a. (1a) Crown attached directly to substrate via an expanded, sometimes stump-like, base 3
- 2b. (1a) Crown attached to substrate via hook-like, prehensile or slender cirri (absent in a few genera) that arise from a single remaining stalk segment, the centrodorsal, which may be discoid, hemispheric, conic or cylindrical COMATULIDA
[NOTE: Comatulids, or feather stars, are unstalked crinoids and are not treated further herein.]
- 3a. (2a) Entire animal reduced to a convex cap or low, rounded cone; IBr (and sometimes also IIBr) series forms a pentagonal vault that closes over the oral surface; arms reduced, not visible when coiled inwards *Cyathidium* Steenstrup 1847 (Fig. 3C)
- 3b. (2a) Calyx stump-like, hollow with thick walls, sometimes expanded upward from its base; rays at least weakly asymmetric, three relatively robust and two more gracile; ten arms coil inward, forming fist-like cover over oral surface *Holopus* Orbigny 1837 (Fig. 3D)
- 4a. (1b) Stalk composed of two or (possibly) a few columnals; rays at least weakly asymmetric, arising obliquely from radial cirlet (Fig. 3A,B) 5
- 4b. (1b) Stalk composed of numerous columnals; crown symmetric, oriented radially on top of stalk (Fig. 1A) 6
- 5a. (4a) Stalk consists of an elongated subcylindrical aboral cup plus a distal conic columnal with an expanded attachment base; radials completely fused, their distal articular faces of the same or similar size, although three rays are longer and more robust than remaining two; arms coil inward over oral surface; proximal brachials roof ambulacra
..... *Gymnocrinus richeri* Bourseau et al. 1987 (Fig. 3A)
- 5b. (4a) Known only from a few short subcylindrical or slightly conic calices; short, lower portion a fused cylinder (perhaps basals, or basals plus uppermost columnal); radials wider and taller with lateral sutures visible, but no clear basal sutures; radial articular faces narrow, the central face much larger than either pair of flanking faces; stalk and arms unknown
Proeudesicrinus lifouensis Améziane-Cominardi and Bourseau (In: Améziane-Cominardi et al., 1990)(Fig. 3B)
- 6a. (4b) Columnals differentiated into nodals bearing segmented cirri, and internodals lacking cirri, at least on proximal part of column (Fig. 1B) 7
- 6b. (4b) Stalk without cirri; no columnals differentiated as nodals 16
- 7a. (6a) Rudimentary, cirrus-bearing nodals restricted to proximal part of stalk; cirrus sockets obliterated distally; stalk terminates in a cementation disk; basals form a short, cylindrical cirlet; radials form a much larger conic cirlet; I and IIBr series of two ossicles each
..... *Proisocrinus ruberrimus* A. H. Clark 1910 (Fig. 4A,B)
- 7b. (6a) Entire stalk consists of well-developed, cirrus-bearing nodals alternating with series of internodals (Fig. 1B); external faces of basals triangular, rhombic or pentagonal, joined as a low cirlet or separated by the radials; IBr and, when present, IIBr series of one to eleven ossicles 8 [PENTACRINITIDAE (including ISOCRINITIDAE)]

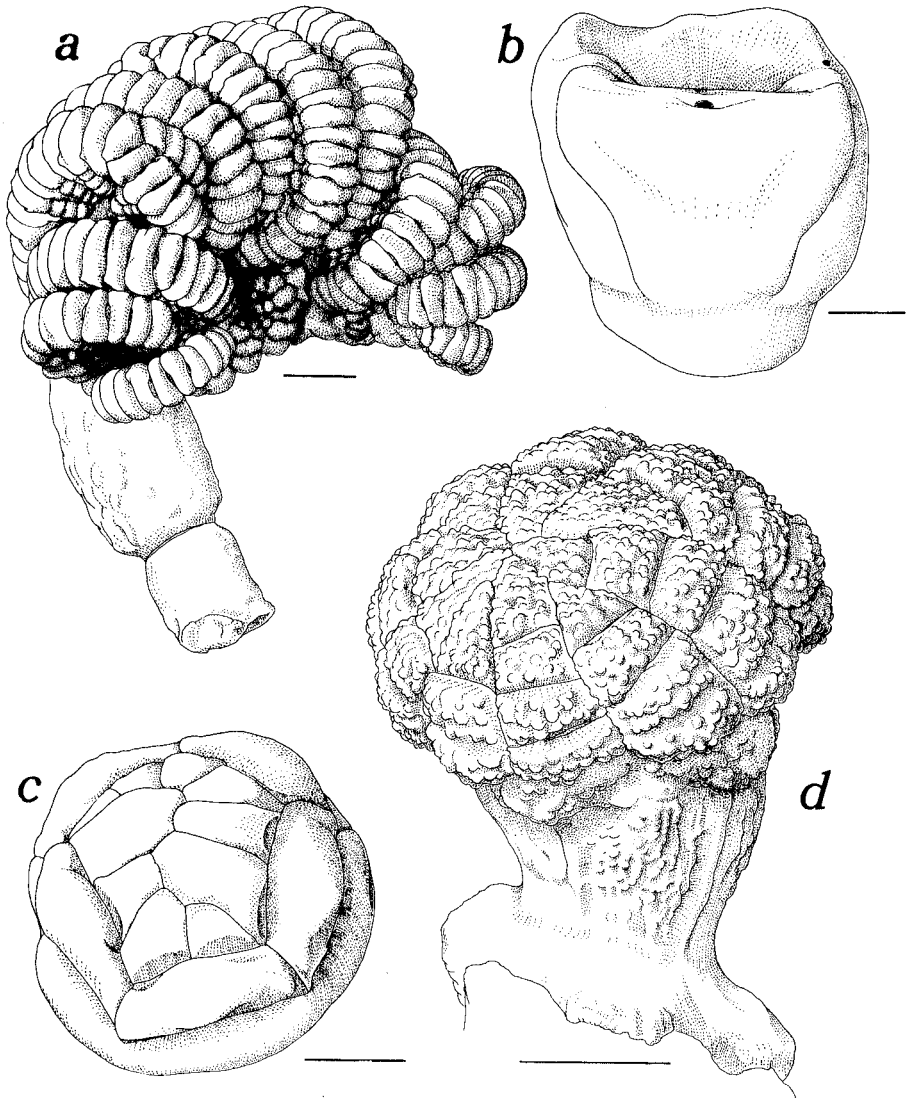


Figure 3. A. *Gymnocrinus richeri* Bourseau et al. (MNHN EcPs 7). Entire specimen, oblique oral view. B. *Proeudesicrinus lifouensis* Cominardi and Bourseau. (MNHN EcPs 40). Aboral cup, oblique lateral view. C. *Cyathidium foresti* Cherbonnier and Guille. (MNHN EcPh 60). Entire animal, oblique oral view. D. *Holopus alidis* Bourseau et al. (PARATYPE, MNHN EcPs 41). Entire specimen, oblique oral view. Scales: A,C,D = 5 mm; B = 1 mm.

- 8a. (7b) IBr series usually of four to seven ossicles (range: two to 11; never two on all five rays) (Fig. 4C,D) 9
- 8b. (7b) IBr series always of two ossicles (e.g., Figs. 5,6) 10
- 9a. (8a) IBr series usually of four ossicles (range: three to six); only first pair of IBr ossicles united by synostosis *Saracrinus* A. H. Clark 1923 (Fig. 4C)
- 9b. (8a) IBr series usually of seven ossicles (range: two to eleven; frequently five in *M. musorstomae*); usually first-second and fourth-fifth ossicles of IBr united by synostoses
..... *Metacrinus* Carpenter 1882 (Fig. 4D)

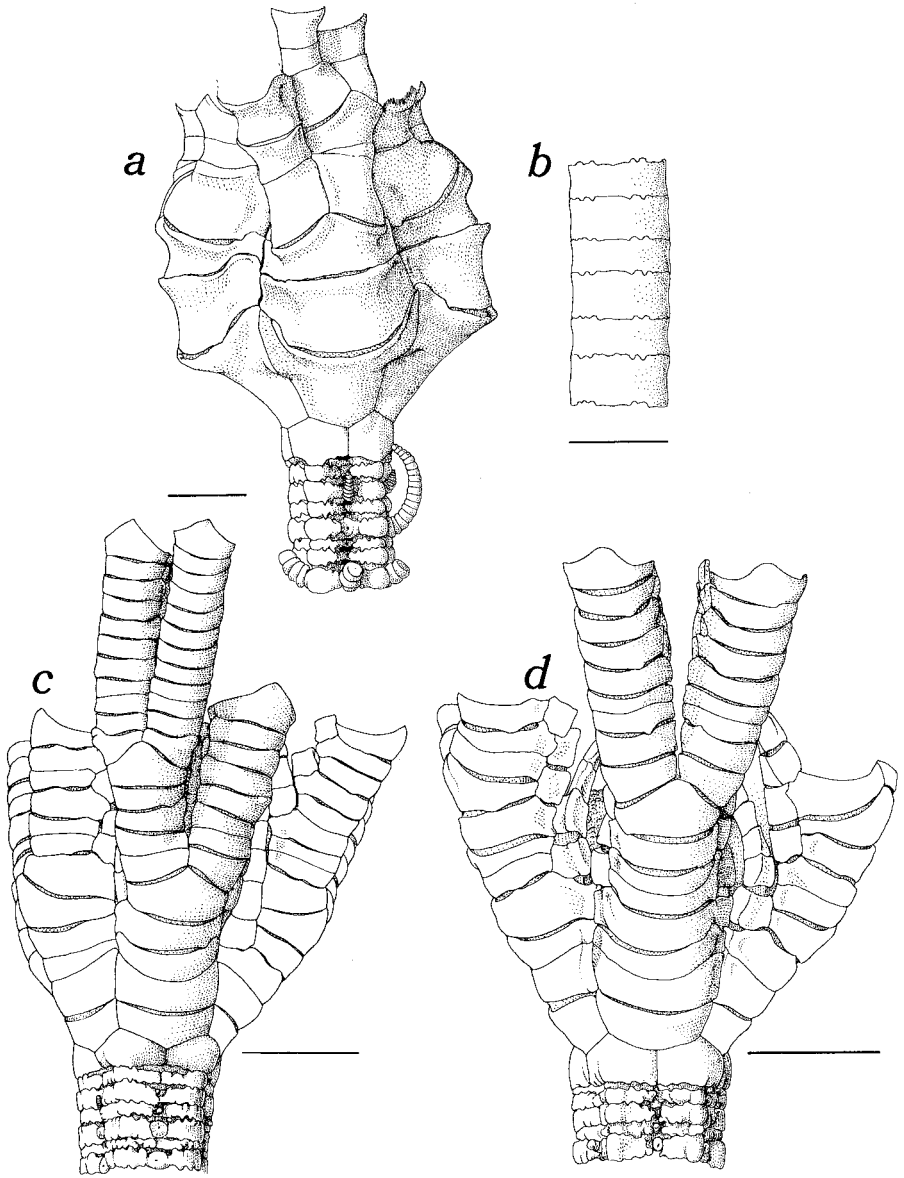


Figure 4. A–B. *Proisocrinus ruberrimus* A. H. Clark. A. Proximal stalk and base of crown, lateral view (Bishop Museum acc. no. 1992.340). B. Portion of mesistele (MNHN EcPs 10247). C–D. Proximal stalk and base of crown, lateral view. C. *Saracrinus nobilis* (Carpenter) (MNHN EcPs 156). D. *Metacrinus levii* Améziere-Cominardi. (MNHN EcPs 63). Scales = 5 mm.

- 10a. (8b) First two ossicles of IBr series united by synarthry or deep symmophy (Fig. 5B); most of stalk (except near crown) cylindrical in cross section; cirri usually weak 11
- 10b. (8b) Two ossicles of IBr series united by synostosis (e.g., Figs. 5E,F,6); most of stalk pentagonal or star-shaped in cross section (rarely cylindric); cirri usually robust 12
- 11a. (10a) Base of crown conic; profile straight or concave; usually more than ten arms
 *Neocrinus* Thomson 1864 (Fig. 5A)

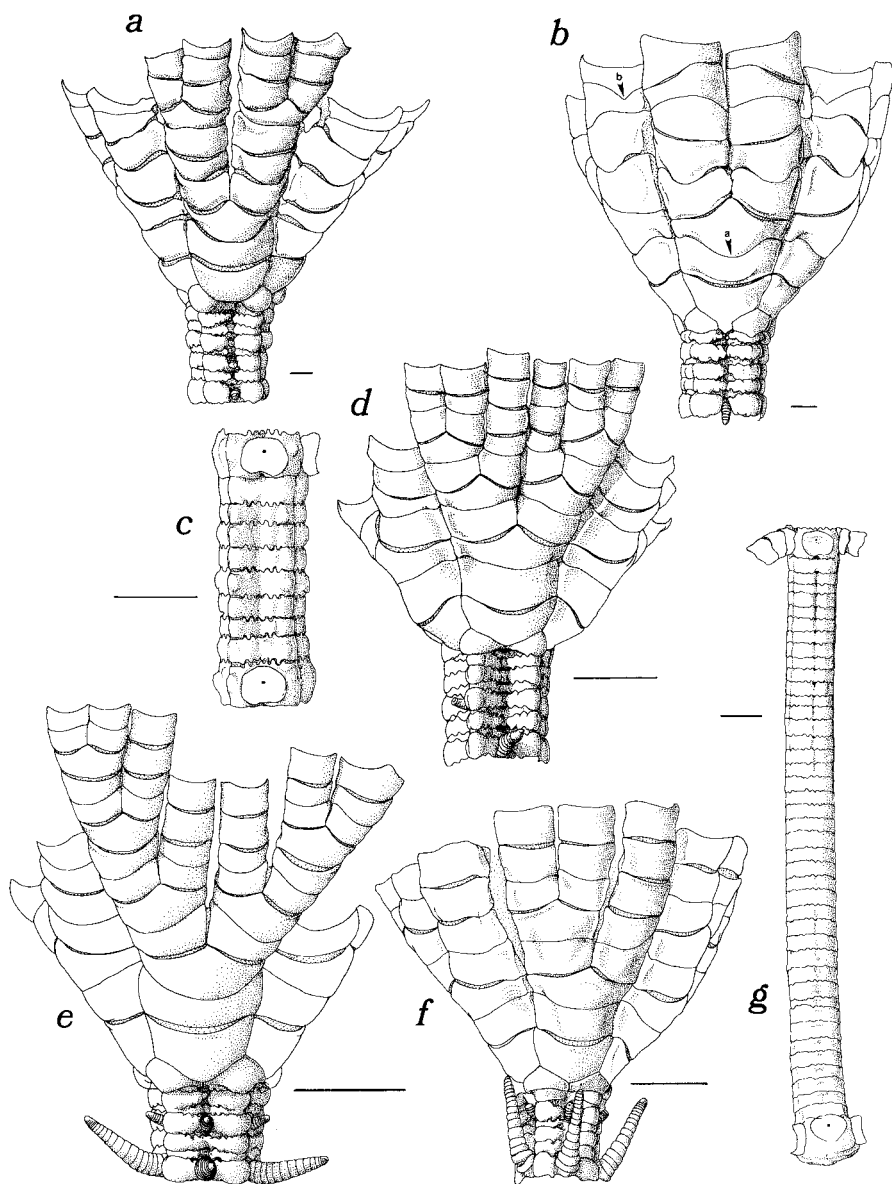


Figure 5. A–B, D–F. Proximal stalk and base of crown, lateral view. A. *Neocrinus decorus* (Thomson). (NSU). B. *Hypalocrinus naresianus* (Carpenter) (MNHN EcPs 203); arrow a: symmorphy; arrow b: transverse symmorphy. D. *Endoxocrinus* (*Diplocrinus*) *alternicirrus* (Carpenter). E. *Endoxocrinus* (*Endoxocrinus*) *muelleri* (Oersted) (NSU CRI 614). F. *Endoxocrinus* (*Annacrinus*) *wyvillethomsoni* (Jeffreys) (MNHN EcPs 1406). C, G. Portion of stalks showing internodal ossicles between two nodals. C. *E. (D.) alternicirrus*. G. *E. (A.) wyvillethomsoni*. Scales: A, B = 1 mm; C–G = 5 mm.

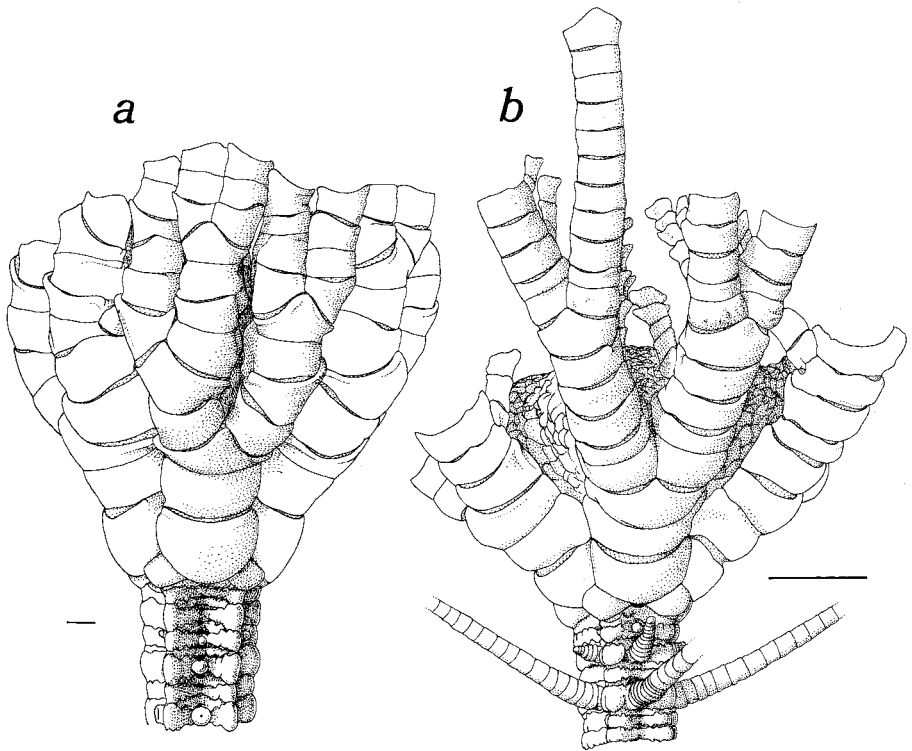


Figure 6. Proximal stalk and base of crown, lateral view. A. *Teliocrinus springeri* (A. H. Clark) (USNM 35995). B. *Cenocrinus asterius* (Linnaeus) (NSU). Scales: A = 1 mm; B = 5 mm.

- 11b. (10a) Base of crown bowl-shaped; profile convex; usually only ten arms
 *Hypalocrinus* A. H. Clark 1908a (Fig. 5B)
- 12a. (10b) IIBr series of two ossicles only (rarely three)
 13 [*Endoxocrinus* A. H. Clark 1908a (Fig. 5C–G)]
- 12b. (10b) IIBr series of more than two ossicles 15
- 13a. (12a) IIIBr and following series of three ossicles, developed exteriorly
 *Endoxocrinus* (*Endoxocrinus*) (Fig. 5E)
- 13b. (12a) IIIBr and following series, when present, of two ossicles only 14
- 14a. (13b) Internodes usually of 12 or fewer columnals
 *Endoxocrinus* (*Diplocrinus*) Döderlein 1912 (Fig. 5C,D)
- 14b. (13b) Internodes long, usually of 20–40 columnals
 *Endoxocrinus* (*Annacrinus*) *wyvillethomsoni* (Jeffreys, 1870) (Fig. 5F,G)
- 15a. (12b) IIBr series usually four ossicles consisting of two pairs united by non-muscular articulation
 *Teliocrinus springeri* (A. H. Clark, 1909a) (Fig. 6A)
- 15b. (12b) IIBr series usually six ossicles (range: 2 to 8); succeeding brachitaxes of more than six ossicles
 *Cenocrinus asterius* (Linnaeus, 1767) (Fig. 6B)
- 16a. (6b) At least some columnals united by synarthry; fulcral ridges of successive articulations not oriented in same plane 17
- 16b. (6b) Synarthries never present in stalk 25
- 17a. (16a) IBr series of two ossicles united by synostosis; ten arms only 18
- 17b. (16a) IBr series with more than two ossicles, or rays unbranched (five arms) 22

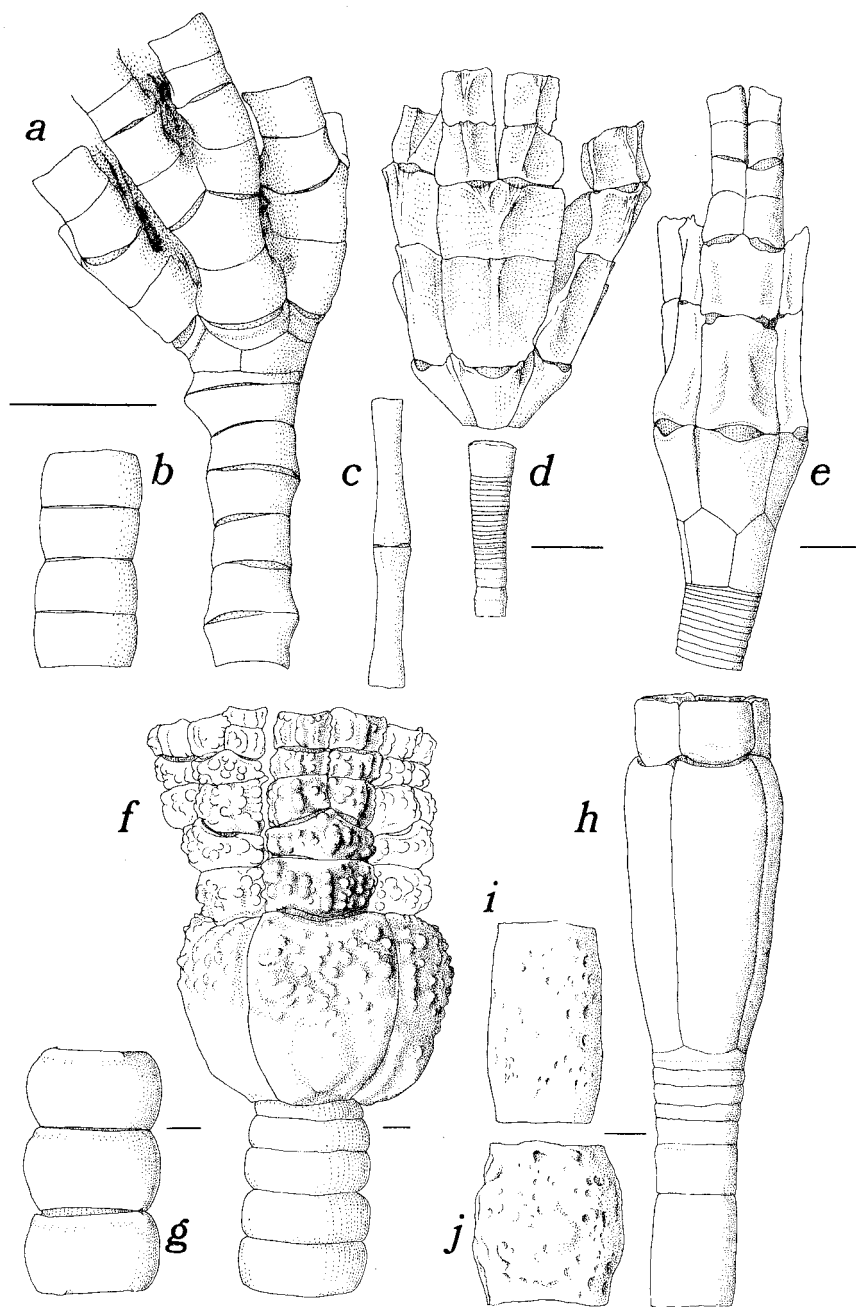


Figure 7. A–B. *Zeuctocrinus gisleni* A. M. Clark (HOLOTYPE, BMNH 1972.12.5.4). A. Proximal stalk and base of crown. B. Four middle columnals. C–D. *Bathycrinus gracilis* Thomson (USNM E16288) C. Two middle columnals. D. Proximal part of stalk and base of crown (crown separated from top of stalk). E. *Monachocrinus recuperatus* (Perrier) (HOLOTYPE, MNHN EcPh 26). Proximal stalk and base of crown. F–G. *Caledonicrinus vaubani* Avocat and Roux (MNHN EcPs 23). F. Proximal stalk and base of crown. G. Three middle columnals. H–J. *Naumachocrinus hawaiiensis* (MNHN EcPs 130). H. Proximal stalk and base of crown. I. Middle columnal. J. Distal columnal. Scales: A–B = 5 mm; C–H = 1 mm. All in lateral view.

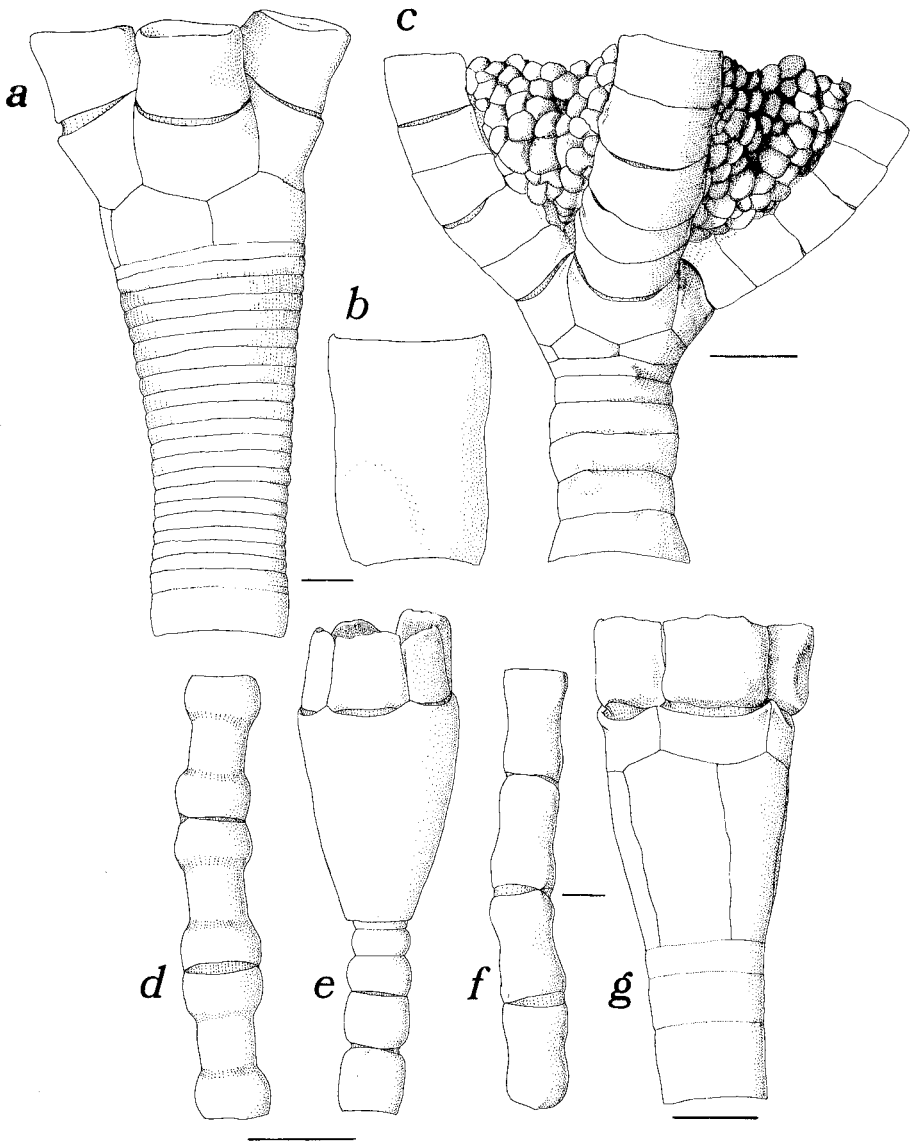


Figure 8. A–B. *Porphyrocrinus thalassae* Roux (MNHN EcPs 238). A. Proximal stalk and base of crown. B. Middle columnal. C. *Phrynocrinus nudus* A. H. Clark (NIWA Z8481). Proximal stalk and base of crown. D–E. *Conocrinus cherbonnieri* Roux (HOLOTYPE, MNHN EcPs 240). D. Three middle columnals. E. Proximal stalk and base of crown. F–G. *Democrinus parfaiti* Perrier (MNHN EcPs 231). F. Four middle columnals. G. Proximal stalk and base of crown. Scales: A–B, D–G = 1 mm; C = 5 mm. All in lateral view.

- 18a. (17a) Calyx composed of both basals and radials (e.g., Figs. 7A,D,E) 19
 18b. (17a) Calyx composed of radials only (Figs. 7F,H) 21
 19a. (18a) Proximal columnal articulations elliptical; middle and distal columnals cylindrical
 *Zeuctocrinus gisleni* A. M. Clark 1973 (Fig. 7A,B)
 19b. (18a) Proximal columnals cylindrical; middle and distal articulations elliptical 20

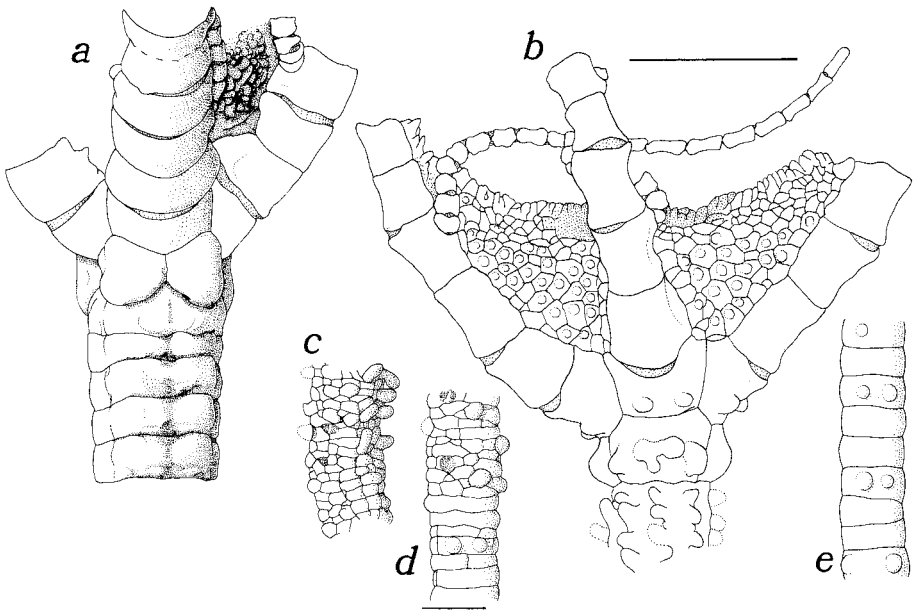
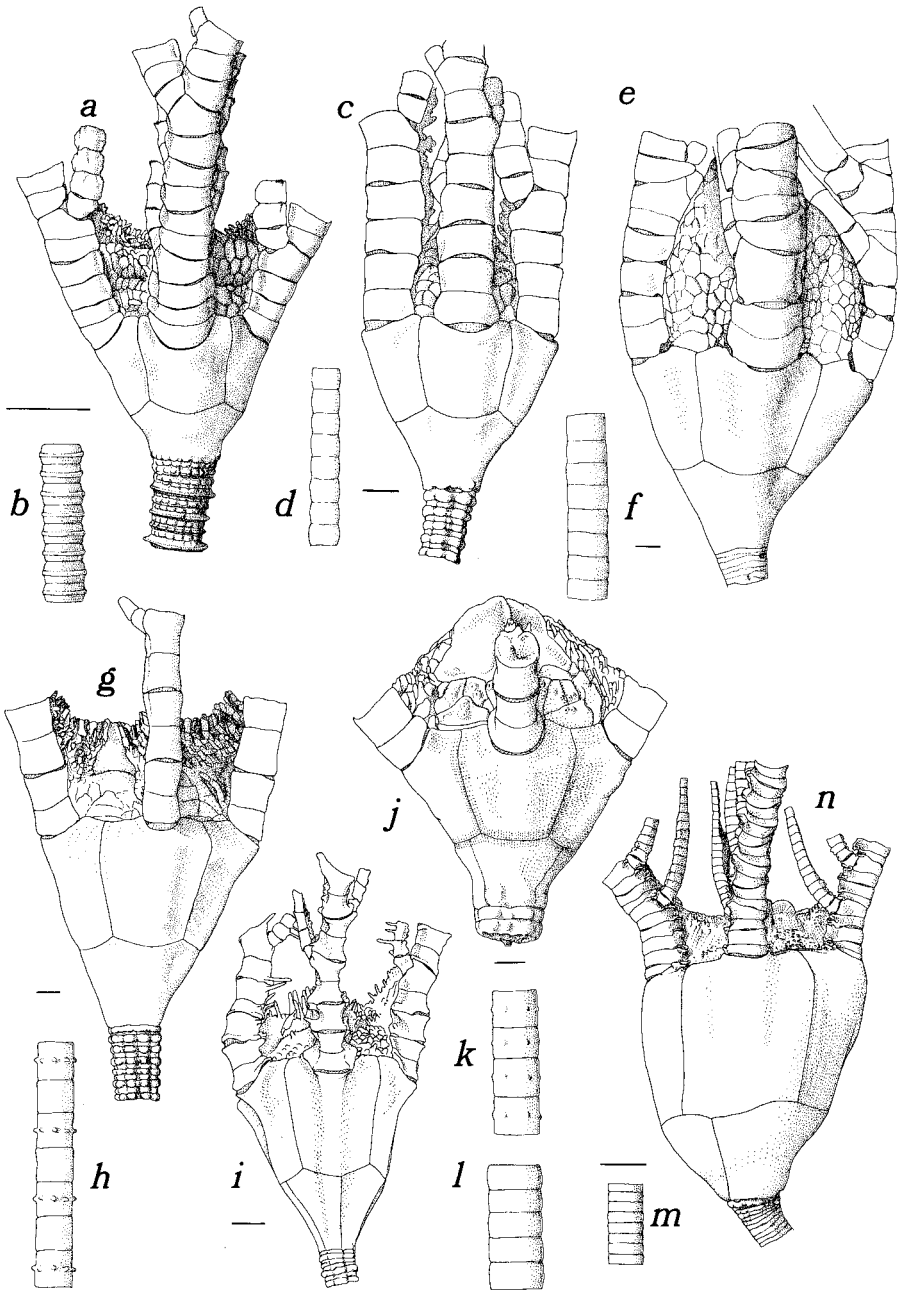


Figure 9. A. *Guillecrinus neocaledonicus* Bourseau et al. (HOLOTYPE, MNHN EcPs 30), Proximal stalk and base of crown, lateral view. B–E. *Vityazicrinus petrachenkoii* Mironov and Sorokina. B. Proximal stalk and base of crown, lateral view. C. Proxistele beginning 5 mm from cup. D. Proxistele beginning 18 mm from cup. E. Mesistele 27 mm from cup. Scales: A–B = 5 mm (upper bar); C–E = 2 mm (lower bar). (B–E redrawn from Mironov and Sorokina, 1998b).

- 20a. (19b) Synostoses between first and second, fourth and fifth, and seventh and eighth brachials of free arm *Bathycrinus* Thomson 1872 (Figs. 7C,D)
- 20b. (19b) Synostoses between first and second, third and fourth, and fifth and sixth brachials of free arm..... *Monachocrinus* A. H. Clark 1917 (Fig. 7E)
- 21a. (18b) Calyx much wider than stalk; radials slightly taller than wide; columnals subcylindric, always wider than tall *Caledonicrinus vaubani* Avocat and Roux (In: Améziane-Cominardi et al., 1990)(Fig. 7F,G)
- 21b. (18b) Calyx little if at all wider than stalk; radials extremely tall and narrow; columnals frequently taller than wide *Naumachocrinus hawaiiensis* A. H. Clark 1912 (Fig. 7H–J)
- 22a. (17b) Sutures between calyx ossicles (radials and basals) clearly distinct; arms five to forty 23
- 22b. (17b) Sutures between calyx ossicles irregular, indistinct; basals frequently fused; only five arms (rays undivided) 24
- 23a. (22a) Numerous very short cylindrical proximal columnals; basals regularly pentagonal; calyx often taller than wide; adjacent IBr series apposed in small specimens; tegmen moderately inflated in large specimens *Porphyrocrinus* Gislén 1925 (Fig. 8A,B)
- 23b. (22a) Short proximal columnals with elliptical articulations; basals short, not regularly pentagonal; calyx much shorter than wide; adjacent IBr series always separated by strongly inflated tegmen *Phrynocrinus nudus* A. H. Clark 1907a (Fig. 8C)
- 24a. (22b) Elliptical distal columnal articulations with ligament fossae forming a short, fat figure eight; articulation between calyx and stalk often constricted *Conocrinus* Orbigny 1850 (Fig. 8D,E)
- 24b. (22b) Elliptical distal columnal articulations with ligament fossae occupying most of articular face; articulation between calyx and stalk never constricted *Democrinus* Perrier 1883 (Fig. 8F,G)



- 25a. (16b) Calyx small, short; basals usually rounded and swollen; radials and following brachials of similar size; pinnules fragile and highly flexible 26
- 25b. (16b) Calyx large, hollow and thin-walled; basals fused or with irregular sutures; radials usually much larger than succeeding ossicles; pinnules well developed, rigid proximally 27
- 26a. (25a) Tegmen without anal tube; arms undivided; five basals; columnal articulations with five to ten deep, usually triangular, ligament fossae *Guillecrinus* Roux 1985 (Fig. 9A)
- 26b. (25a) Tegmen with well developed anal tube; arms divided at Br7; three basals; columnal articulations without deep ligament fossae
..... *Vityazicrinus petrachenkoi* Mironov and Sorokina 1998b (Fig. 9B–E)
- 27a. (25b) Arms branch beyond IBr10 in each ray; tegmen strongly inflated; proximal part of P₁ attached to tegmen *Calamocrinus diomedea* Agassiz 1890 (Figs. 10A,B).
- 27b. (25b) Arms normally unbranched; tegmen flat or inflated, but never incorporating base of P₁ 28
- 28a. (27b) First pinnule on Br4; second synostosis between the fifth and sixth brachials 29
- 28b. (27b) First pinnule generally arises distal to Br4; second synostosis between third and fourth or between fourth and fifth brachials 30
- 29a. (28a) Pinnules closely resemble juvenile arms; columnal symplexies with seven small crenulae *Gephyrocrinus grimaldii* Koehler and Bather 1902 (Figs. 10C,D)
- 29b. (28a) Pinnules normally elongated, not at all resembling juvenile arms; columnal symplexies with seven or more well-developed crenulae *Ptilocrinus* A. H. Clark 1907b (Fig. 10E,F)
- 30a. (28b) First pinnule usually at Br5; never series of more than two brachials united by synostosis before Br11; columnal symplexies with units of two or more well developed crenulae 31
- 30b. (28b) Location of first pinnule variable (Br4 to Br7); usually series of more than two brachials united by synostosis before Br11; columnal symplexies with units of one, rarely two small crenulae *Hyocrinus* Thomson 1876 (Fig. 10G,H)
- 31a. (30a) Calyx conic; proximal stalk hexagonal in cross section; columnal symplexies with six units of two or three small crenulae *Thalassocrinus* A. H. Clark 1911 (Figs. 10I–L)
- 31b. (30a) Calyx hemispheric; proximal stalk circular in cross section; columnal symplexies with a well-developed, multiradiate crenularium
..... *Anachalypsicrinus* A. M. Clark 1973 (Figs. 10M,N)

KEY 2. STALKS OF LIVING STALKED CRINOIDS

- 1a. Stalk composed of two (or possibly a few) columnals 2
- 1b. Stalk composed of many columnals 3
- 2a. (1a) Stalk consists of two pieces: an elongated subcylindric aboral cup with all radial articular faces of the same size, and a distal conic columnal with an expanded attachment base
..... *Gymnocrinus richeri* (Fig. 3A)
- 2b. (1a) Known only from a few short subcylindric or slightly conic calices; short, lower portion a fused cylinder [perhaps basals, or basals plus uppermost columnal]; the central radial articular face much larger than either pair of flanking faces; complete stalk unknown
..... *Proeudesicrinus lifouensis* (Fig. 3B)

Figure 10. (opposite page) A–B. *Calamocrinus diomedea* Agassiz (USNM E47881). A. Proximal stalk and base of crown. B. Eight middle columnals. C–D. *Gephyrocrinus grimaldii* Koehler and Bather (MNHN EcPs 245). C. Proximal stalk and base of crown. D. Eight middle columnals. E–F. *Ptilocrinus pinnatus* A. H. Clark (COTYPE, MNHN EcPs 237). E. Proximal stalk and base of crown. F. Eight middle columnals. G–H. *Hyocrinus cyanae* Bourseau et al. (MNHN EcPs 244) G. Proximal stalk and base of crown. H. Seven middle columnals. I. *Thalassocrinus alvinae* Roux (HOLOTYPE, USNM E36051), Proximal stalk and base of crown. J–L. *Thalassocrinus pontifer* A. H. Clark (HOLOTYPE, USNM 27483). J. Proximal stalk and base of crown. K. Four middle columnals. L. Five distal columnals. M–N. *Anachalypsicrinus nefertiti* A. M. Clark (HOLOTYPE, BMNH 1972.12.5.1). M. Eight middle columnals. N. Proximal stalk and base of crown. Scales: A–B, M–N = 5 mm; C–H, J–L = 1 mm; I = 2 mm. All in lateral view.

3a. (1b) Homeomorphic stalk	4
3b. (1b) Heteromorphic or xenomorphic stalk	7
4a. (3a) Mid-stalk columnals with 5–10 deep ligament fossae	<i>Guillecrinus</i>
4b. (3a) Mid-stalk columnals lacking ligament fossae	5
5a. (4b) Proximal stalk with numerous discoid columnals having complex external ornamentation	<i>Vityazicrinus petrachenkoi</i> (Fig. 9B–E)
5b. (4b) Proximal stalk without complex external ornamentation; columnal articulations with usually more than 5 crenular units	6 [HYOCRINIDAE]
6a. (5b) Proximal stalk section regularly hexagonal; symplexies with 6 crenular units	<i>Thalassocrinus</i>
6b. (5b) Proximal stalk never hexagonal; symplexies with usually more than 6 crenular units	[Other genera of HYOCRINIDAE]
7a. (3b) Heteromorphic stalk differentiated into nodals and internodals; cirri present at least proximally; symplexies with pentamerous symmetry	8
7b. (3b) Xenomorphic stalk with synarthrial articulations; nodals and cirri never present	9
8a. (7a) Cirrus-bearing nodals along entire length	[PENTACRINITIDAE (including ISOCRINIDAE)]
8b. (7a) Weak cirri developed only proximally; middle and distal stalk consists of nodals lacking cirri (nudinodals) and internodals	<i>Proisocrinus ruberrimus</i> (Figs. 4A,B)
9a. (7b) Proximal stalk with numerous low cylindrical columnals	10
9b. (7b) Proximal stalk with a few or without low cylindrical columnals	11
10a. (9a) Proximal stalk articulations with pentamerous symmetry	<i>Porphyrocrinus</i>
10b. (9a) Proximal stalk articulations with undivided flat facets	<i>Bathycrinus</i>
11a. (9b) First proximal stalk articulations are synarthries	12
11b. (9b) First proximal stalk articulations are flat synostoses	13
12a. (11a) Distal columnals subcylindric and articulated by synarthries without deep ligament fossae	<i>Zeutocrinus</i>
12b. (11a) Distal columnals never cylindric, articulated by elliptic synarthries with deep ligament fossae	<i>Phrynocrinus</i>
13a. (11b) Middle and distal columnals articulated by synarthries without deep ligament fossae ..	<i>Caledonicrinus</i> and <i>Naumachocrinus</i>
13b. (11b) Middle and distal columnals articulated by synarthries with deep ligament fossae	14
14a. (13b) Synarthries of distal columnals with fossae forming a short, fat figure eight in the center of the ligament area	<i>Conocrinus</i>
14b. (13b) Distal elliptic synarthries with large deep fossae covering the entire ligament area	<i>Democrinus</i>

LIST OF NOMINAL SPECIES OF LIVING STALKED CRINOIDS

The following list of genera includes all currently recognized nominal species and their general geographical ranges. The combination of generic keys, species list and literature cited provides the most current available set of tools for identification of living stalked crinoids. Those interested in greater taxonomic detail and original descriptions may consult cited references given in the 'Remarks' sections below.

Genera with only the 'type species' listed are considered monospecific. Fossil taxa, indicated by a dagger (†) and stratigraphic range rather than geographic distribution, are included only if they are 'type species' of a genus.

Family HOLOPODIDAE Zittel, 1879

Remarks.—Améziane et al. (1999) revised the living members of the family in detail.

Cyathidium Steenstrup, 1847

Type species.—†*Cyathidium holopus* Steenstrup, 1847 (Paleocene).

Other included species.—*Cyathidium foresti* Cherbonnier and Guille, 1972 (Northern mid-Atlantic seamounts) (Fig. 3C); *Cyathidium plantei* Heinzeller et al., 1996 (SW tropical Indian); *Cyathidium pourtalesi* Améziane et al., 1999 (NW tropical Atlantic).

Holopus Orbigny, 1837

Type species.—*Holopus rangii* Orbigny, 1837 (W tropical Atlantic).

Other included species.—*Holopus alidis* Bourseau et al., 1991 (SW tropical Pacific) (Fig. 3D).

Family HEMICRINIDAE Rasmussen, 1961

Gymnocrinus Loriol, 1879

Type species.—†*Gymnocrinus moeschi* Loriol, 1879 (Upper Jurassic).

Other included species.—*Gymnocrinus richeri* Bourseau et al., 1987 (SW tropical Pacific) (Fig. 3A).

Remarks.—See Bourseau et al. (1991) for a discussion of *G. richeri*.

Family EUDESICRINIDAE Bather, 1899

Proeudesicrinus Cominardi and Bourseau, 1990.

Type species.—*Proeudesicrinus lifouensis* Cominardi and Bourseau (In: Améziane-Cominardi et al. 1990) (SW Pacific [New Caledonia]) (Fig. 3B).

Family MILLERICRINIDAE Jaekel, 1918

Proisocrinus A. H. Clark, 1910

Type species.—*Proisocrinus ruberrimus* A. H. Clark, 1910 (W and central Pacific) (Fig. 4A,B).

Remarks.—See Bourseau et al. (1991) and David (1998).

Family PENTACRINITIDAE Gray, 1842

Remarks.—A. H. Clark (1923) and Bourseau et al. (1991) attributed all modern pentacrinids to the family Pentacrinidae sensu lato (including Isocrinidae Gislén 1924; but see Rasmussen and Sieverts-Doreck 1978 and Simms 1988 for alternatives). For additional information, see David (1998) for *Cenocrinus* and *Neocrinus*; Bourseau and Roux

(1989) for *Hypalocrinus*; Roux (1981) and Améziane-Cominardi (1991) for *Metacrinus* and *Saracrinus*, and Roux (1976a), Macurda and Roux (1981), David (1998) and David & Roux (2000b) for *Endoxocrinus*.

Cenocrinus Thomson, 1864

Type species.—*Isis asteria* Linnaeus, 1767 (W tropical Atlantic) (Fig. 6B).

Endoxocrinus (*Endoxocrinus*) A. H. Clark, 1908a

Type species.—*Pentacrinus muelleri* Oersted, 1857 (W tropical Atlantic) (Fig. 5E).

Other included species.—*Diplocrinus carolinae* A. H. Clark, 1934; *Endoxocrinus prionodes* H. L. Clark, 1941 (both W tropical Atlantic).

Endoxocrinus (*Annacrinus*) A. H. Clark, 1923

Type species.—*Pentacrinus wyvillethomsoni* Jeffreys, 1870 (NE Atlantic) (Fig. 5F,G).

Endoxocrinus (*Diplocrinus*) Döderlein, 1912

Type species.—*Pentacrinus maclearanus* Thomson, 1878 (W tropical Atlantic).

Other included species.—*Pentacrinus alternicirrus* Carpenter, 1884 (Fig. 5C,D); *Pentacrinus sibogae* Döderlein, 1907 (both W tropical Pacific).

Hypalocrinus A. H. Clark, 1908a

Type species.—*Pentacrinus naresianus* Carpenter, 1882 (W tropical Pacific) (Fig. 5B).

Remarks.—Bourseau and Roux (1989) gave a detailed analysis of morphological variation in *H. naresianus*.

Metacrinus Carpenter, 1882

Type species.—*M. wyvillii* Carpenter, 1884 (W Pacific).

Other included species.—*M. costatus* Carpenter, 1884; *M. interruptus* Carpenter, 1884; *M. levii* Améziane-Cominardi, 1990 (in Améziane-Cominardi et al., 1990) (Fig. 4D); *M. musorstomae* Roux, 1981; *M. nodosus* Carpenter, 1884; *M. rotundus* Carpenter, 1885; *M. serratus* Döderlein, 1907; *M. zonatus* A. H. Clark, 1908b (all W Pacific).

Remarks.—Améziane-Cominardi (1991) and Bourseau and Roux (1989) offered detailed discussions of morphology and distribution of *Metacrinus*.

Neocrinus Thomson, 1864

Type species.—*Pentacrinus decorus* Thomson, 1864 (W tropical Atlantic) (Fig. 5A).

Other included species.—*Pentacrinus blakei* Carpenter, 1884 (W tropical Atlantic).

Remarks.—Most recent references place *Neocrinus decorus* in *Chladocrinus* and *N. blakei* in *Isocrinus* following Rasmussen and Sieverts-Doreck (1978). Based on ontogenetic studies, Améziane and Roux (1994) and David (1998) concluded that the two spe-

cies belong to a single genus different from the Jurassic *Chladocrinus* and *Isocrinus*. We have returned both to *Neocrinus* pending detailed re-examinations of the other, now exclusively fossil, genera. Donovan (1984) and Messing (1985) discussed details of stem morphology and local distribution, respectively, of *N. decorus*.

Saracrinus A. H. Clark, 1923

Type species.—*Metacrinus nobilis* Carpenter, 1884 (W Pacific) (Fig. 4C).

Other included species.—*Metacrinus angulatus* Carpenter, 1884; *S. moosai* Améziane, 1997; *Metacrinus varians* Carpenter, 1884 (all W Pacific).

Remarks.—Améziane-Cominardi (1991), Améziane (1997) and Bourseau and Roux (1989) discussed morphology and distribution of *Saracrinus* in detail.

Teliocrinus Döderlein, 1912

Type species.—*Hypalocrinus springeri* A. H. Clark, 1909a (N Indian) (Fig. 6A).

Remarks.—See Oji (1990) for synonyms.

Family HYOCRINIDAE Carpenter, 1884

Remarks.—See A. M. Clark (1973), Mironov and Sorokina (1998a,b), Roux (1980 and in press) and Roux and Pawson (1999).

Anachalypsicrinus A. M. Clark, 1973

Type species.—*Anachalypsicrinus nefertiti* A. M. Clark, 1973 (NE Atlantic) (Fig. 10M,N).

Other included species.—*Ptilocrinus atlanticus* Roux, 1990 (NW Atlantic [off Newfoundland]).

Calamocrinus Agassiz, 1890

Type species.—*Calamocrinus diomedeeae* Agassiz, 1890 (E Pacific [Galápagos Is.]) (Fig. 10A,B).

Remarks.—See Holland et al. (1991) for a detailed histological study.

Gephyrocrinus Koehler and Bather, 1902

Type species.—*Gephyrocrinus grimaldii* Koehler and Bather, 1902 (N Atlantic) (Fig. 10C,D).

Hyocrinus Thomson, 1876

Type species.—*Hyocrinus bethellianus* Thomson, 1876 (SW Indian).

Other included species.—*Hyocrinus cyanae* Bourseau et al., 1991 (SW tropical Pacific) (Fig. 10G,H); *Hyocrinus foelli* Roux and Pawson, 1999 (Central and NE Pacific); *Hyocrinus giganteus* Roux and Pawson, 1999 (Central Pacific [Horizon Seamount]);

Belyaevicrinus latipinnulus Mironov and Sorokina, 1998b (Southern Ocean [E of the Antarctic Peninsula]); *Thalassocrinus (Conferocrinus) depauperatus* Mironov and Sorokina, 1998b (NE Indian).

Ptilocrinus A. H. Clark, 1907b

Type species.—*Ptilocrinus pinnatus* A. H. Clark, 1907b (E Pacific) (Fig. 10E,F).

Other included species.—*Ptilocrinus ahearnae* Mironov and Sorokina, 1998b (NW Pacific); *P. antarcticus* Bather, 1908 (Southern Ocean [W of the Antarctic Peninsula]); *P. brucei* Vaney (In: Vaney and John 1939)(Southern Ocean [E of the Antarctic Peninsula]); *Ailsacrinus pteripterus* Mironov and Sorokina, 1998a (N Pacific); *P. perforatus* Mironov and Sorokina, 1998b (SW Atlantic); *P. stukalinae* Mironov and Sorokina, 1998b (NW Pacific).

Thalassocrinus A. H. Clark, 1911

Type species.—*Thalassocrinus pontifer* A. H. Clark, 1911 (W tropical Pacific) (Fig. 10J–L).

Other included species.—*Thalassocrinus clausus* Mironov and Sorokina, 1998b; *T. mironovi* Roux, 2002 (both W tropical Pacific); *T. alvinae* Roux, 2002 (NE Pacific [Gorda Ridge]) (Fig. 10I).

Family BATHYCRINIDAE Bather, 1899

Remarks.—See Macurda and Meyer (1976), Roux (1977), and Duco and Roux (1981)

Bathycrinus Thomson, 1872

Type species.—*Bathycrinus gracilis* Thomson, 1872 (NE Atlantic) (Fig. 7C,D).

Other included species.—*B. aldrichianus* Thomson, 1876 (S Atlantic); *B. australis* A. H. Clark, 1907b (SW Atlantic, S Indian, off New Zealand); *B. australocrucis* McKnight, 1973 (off New Zealand); *Ilycrinus carpenteri* Danielssen and Koren, 1877 (Norwegian Sea and Arctic Ocean); *B. complanatus* A. H. Clark, 1907c (NW Pacific); *B. equatorialis* A. H. Clark, 1908c (E central Pacific); *B. pacificus* A. H. Clark, 1907a (NW Pacific [off Japan]); *B. sibogae* A. H. Clark, 1917 (Indonesia); *B. woodmasoni* A. H. Clark, 1909c (NE Indian).

Caledonicrinus Avocat and Roux (In: Améziame-Cominardi et al., 1990)

Type species.—*Caledonicrinus vaubani* Avocat and Roux (In: Améziame-Cominardi et al., 1990) (SW Pacific) (Fig. 7F,G).

Remarks.—See Bourseau et al. (1991) for a complete description.

Monachocrinus A. H. Clark, 1917

Type species.—*Ilyocrinus recuperatus* Perrier, 1885 (NE Atlantic) (Fig. 7E).

Other included species.—*Monachocrinus aotearoa* McKnight, 1973 (off New Zealand); *Bathycrinus caribbeus* A. H. Clark, 1908c (W tropical Atlantic); *M. coelus* H. L. Clark, 1923 (SE Atlantic); *M. mortenseni* Gislén, 1938 (SW Pacific [New Caledonia]); *Bathycrinus paradoxus* A. H. Clark, 1909c (NE Indian [Bay of Bengal]); *M. sexradiatus* A. H. Clark, 1923b (N Atlantic).

Naumachocrinus A. H. Clark, 1912

Type species.—*Naumachocrinus hawaiiensis* A. H. Clark, 1912 (SW and central Pacific) (Figs. 7H–J).

Remarks.—See Bourseau et al. (1991).

Zeuctocrinus A. M. Clark, 1973

Type species.—*Zeuctocrinus gisleni* A. M. Clark, 1973 (NE Atlantic) (Figs. 7A,B).

Remarks.—See Roux (1977) for stalk morphology.

Family BOURGUETICRINIDAE Loriol, 1882

Remarks.—See Roux (1976b, 1977).

Conocrinus Orbigny, 1850

Type species.—†*Bourgueticrinus thorenti* d'Archiac, 1846 (Eocene).

Other included species.—*Conocrinus cabiochi* Roux, 1976b (NE Atlantic); *C. cherbonnieri* Roux, 1976b (NE Atlantic) (Figs. 8D,E); *Rhizocrinus lofotensis* Sars, 1868 (N Atlantic); *Democrinus globularis* Gislén, 1925; *Bathycrinus minimus* Döderlein, 1907; *Bathycrinus poculum* Döderlein, 1907 (all Indonesia).

Democrinus Perrier, 1883

Type species.—*Democrinus parfaiti* Perrier, 1883 (NE Atlantic) (Figs. 8F,G).

Other included species.—*D. aoteanus* McKnight, 1973 (off New Zealand); *Rhizocrinus brevis* A. H. Clark, 1909b; *R. conifer* A. H. Clark, 1909b; *R. rawsonii* Pourtalès, 1874 (all W tropical Atlantic); *R. (Bythocrinus) chuni* Döderlein, 1907 (W Indian); *D. japonicus* Gislén, 1927 (NW Pacific); *Bathycrinus nodipes* Döderlein, 1907 (Indonesia); *R. weberi* Döderlein, 1907 (Philippines and Indonesia).

Family PHRYNOCRINIDAE A. H. Clark, 1907a

Remarks.—See A. M. Clark (1973), Roux (1977) and Donovan and Pawson (1994).

Phrynocrinus A. H. Clark, 1907a

Type species.—*Phrynocrinus nudus* A. H. Clark, 1907a (W Pacific) (Fig. 8C).

Porphyrocrinus Gislén, 1925

Type species.—*Porphyrocrinus verrucosus* Gislén, 1925 (W Pacific).

Other included species.—*Monachocrinus incrassatus* Gislén, 1933 (NE and S central Atlantic); *Porphyrocrinus polyarthra* A. M. Clark, 1973 (SW Indian); *P. thalassae* (Roux 1977) (NE Atlantic) (Fig. 8A,B).

Family GUILLECRINIDAE Mironov and Sorokina, 1998b

Guillecrinus Roux, 1985

Type species.—*G. reunionensis* Roux, 1985 (W Indian [Reunion I.]).

Other included species.—*G. neocaledonicus* Bourseau et al., 1991 (SW Pacific) (Fig. 9A).

Family VITYAZICRINIDAE Mironov and Sorokina, 1998b

Vityazicrinus Mironov and Sorokina, 1998b

Type species.—*V. petrachenkoi* Mironov and Sorokina, 1998b (Central Pacific) (Figs. 9B–E).

ACKNOWLEDGMENTS

We would like to thank D. Pawson (Smithsonian Institution) and S. Halsey (Natural History Museum, London) for providing access to specimens for illustrations, and X. Drothière, C. Radet (Université de Reims), F. Devienne and M. Grasset (Université Paris VI) for technical assistance. We would also like to thank D. Meyer (University of Cincinnati), S. Donovan (Natural History Museum, London) and two other unidentified reviewers for their careful and thorough reviews of the manuscript. Specimens in the Nova Southeastern University Oceanographic Center collection were collected as part of NSF grant EAR-9628215. Many of the illustrations were completed by the second author while a Visiting Scientist at the Muséum national d'Histoire naturelle, Paris, in July 1998.

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DATE SUBMITTED: September 8, 2000.

DATE ACCEPTED: July 9, 2001.

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