# Towards a systematic standard approach to describing fossil crinoids, illustrated by the redescription of a Scottish Silurian *Pisocrinus* de Koninck

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Systematic taxonomy requires thoughtful, detailed and structured descriptions of species characters, and essential additional data for effective comparison with other specimens. Crinoid terminology is commonly misused or at best confused. The purpose of this paper is to facilitate this process by encouraging a standard methodology which would make comparisons of fossil crinoid taxa easier for all. An ordered tabulation of those characters that should be considered in any description of a fossil crinoid is provided and implemented in describing a Scottish Llandovery (Lower Silurian) disparid crinoid *Pisocrinus* cf. *campana* S.A. Miller.

## Contents



## Introduction

The form and precise terminology of systematic descriptions are the primary vehicles for recording information concerning the morphology of fossils. Progress in palaeontology may be hampered by imprecision and variability in the way taxa are described, that is, produced by a lack of regularised structure. The importance of clear, precise and comprehensive descriptions of fossil specimens and species has long been advocated (e.g., Raup & Stanley, 1978, pp. 27-44). Riedel (1978) highlighted the importance of using morphogenic descriptors to improve the stability of definitions, which permit postponement of species identification until morphology has been properly delimited. This enables reliable transmission of information on taxa, avoids incorrect identification and facilitates modifications by future authors describing new, better preserved specimens. Systems of morphologic descriptors can serve as useful tools for postponing the erection of a taxonomic system to accommodate a group of fossils whose phyletic relationships are not yet thoroughly understood. Precise morphologic descriptors provide a firm foundation on which to build (Table 1).

Table 1. Checklist of morphological features for describing fossil crinoids.

| | | |
|---|---|---|
| **1.** | **Crown shape** | small / medium / large<br>slender / robust<br>rotund / sub-spherical / conical / elongate<br>shuttlecock-shaped (Fig. 1.) |
| | *crinoid design*<br>(see Ausich,1988) | multiplated bowl<br>multiplated bicone<br>conical mosaic<br>urn<br>cylinder<br>cone<br>ellipsoid<br>hand<br>bowl<br>bilaterally recumbent<br>fist-shaped |
| **2.** | **Aboral cup** | small / medium / large<br>monocyclic / dicylic / cryptodicyclic / other<br>high / medium / low / flat<br>cone / bowl / globose / conico-cylindrical / 'egg- shaped' / tubular (Fig. 1) |
| | *plan view* | circular / pentalobate |
| | *ratio of height to width* | tall / medium / short<br>saucer-shaped / narrow / wide |
| | *measurements* | height<br>calyx diameter through A ray to CD interray<br>radius of CD interray<br>radius of C ray<br>radius of A ray<br>radius of *AB interray* |
| | *symmetry* | radial / bilateral / asymmetrical |
| | *column diameter relative to cup* | narrow / wide |
| | *most proximal columnal distinct from cup* | yes / no |
| | *shape of base* | convex / flat / discoidal<br>truncated / depressed |
| | *cup plate sculpture* | smooth / spinose / wrinkled / ridged / granular fluted / pitted / nodose / pustulose |
| | *stellate ridges* | single or paired / few multiple / numerous |
| | *basal circlet* | flat / concave / convex<br>circular / subcircular / triangular<br>diameter |
| | *infrabasal circlet* | unseen / concealed / down-flaring / upflaring |
| **3.** | **Infrabasals (IBB)** | absent / hidden by proximal columnal<br>visible in side view / not visible in side view<br>equal height / un-equal height<br>2 / 3 / 4 / 5 / small / prominent<br>upflared / horizontal / downflared |
| **4.** | **Basals (BB)** | small / medium / large<br>pentagonal base / quadripartite hexagonal base / tripartite base |
| | *hexagonal*<br>*pentagonal* | interrupted by anal series<br>anal series lies above the upper circlet |

| | | |
|---|---|---|
| | *number of basals* | 1 / 2 / 3 / 4 / 5 / more than 5 |
| | *sculpture* | smooth / spinose / wrinkled / ridged / granular fluted / pitted / nodose / pustulose |
| 5. | **Radials (RR)** | small / medium / large<br>equal / sub-equal<br>tall / short<br>higher than width / equal to width / shorter than width<br>hexagonal / quadrangular / triangular<br>incontact laterally / separated |
| | *measurements* | radial plate height<br>radial plate width |
| | *sculpture* | smooth / spinose / wrinkled / ridged / granular fluted / pitted<br>nodose / pustulose |
| | *biradials*<br>*superradial (upper)* | <br>bigger than inferradial/smaller than inferradial<br>absent / present<br>small / large / high / low<br>equal / sub-equal / shape<br>angustary / peneplenary / plenary / declinate |
| | *inferradial (lower)* | bigger than superradial/smaller than superradial<br>absent / present<br>small / large / high / low<br>equal / sub-equal / shape<br>angustary / peneplenary / plenary / declinate |
| | *width of radial facets relative to width of radial* | narrow / intermediate / wide |
| | *radial facets* | differentiated / similar<br>circular / oval / horseshoe<br>angustary / peneplenary / plenary / declinate<br>smooth / sculptured<br>shallow concave surfaces<br>absence / presence of culmina on outer margin<br>absence / presence of crenullae on outer margin<br>traces of transverse ridge and dorsal ligament pit [synarthrial]<br>no traces of transverse ridge and dorsal ligament |
| | *radial processes* | absent / present<br>spear-shaped (lanceolate)/ square-shaped (cuboid) |
| 6. | **Tegmen** | unknown / known<br>robust and heavily plated / thin or unmineralised<br>rigid / apparently non-rigid<br>description of shape if different from anal sac |
| | *anal series* | globose / dome / tubular / mushroom-shaped / sac |
| 7. | **Orals** | small / large / slender / robust<br>ribbed / nodose / tessellate / flexible / hexagonal<br>spinose<br>CD oral larger than/same size as other orals |
| 8. | **Radianal** | *Interradianal in contact with anal X* yes / no |
| | *interradials* | absent / present<br>small / large<br>single range / 2 or more / ordered<br>unconnected to tegmen / connected to tegmen<br>depressed / expanding to tegmen |

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| **9. Anal series** | |
| *anal X* | absent / present<br>height relative to width |
| *anal X location* | directly on C ray or superradial / directly on fused B and C superradials / most proximal C ray plate / on the left shoulder of an undivided C radial which supports an arm on its right shoulder / on left shoulder of $3^{rd}$ C-ray plate.<br>position of anal x above radianal |
| *plated peristome* | absent / present |
| **10. Accessory plates** | absent / present |
| | number? shape? |
| **11. Articulation between calyx plates** | zygosynostosial / symplexial fused in ankylosis (Fig. 2D) |
| **12. Arms** | None/ less than 5 / 5 / 10 / 20 / 40 / more than 40<br>type of articulation<br>fixed / free<br>equal / unequal<br>fixed brachials / fixed pinnules<br>interbrachials / interpinnules |
| *primibrachials* | 1 / 2 / 3 / 4 / 5 or more |
| *measurements* | $1^{st}$ primibrachial height: $1^{st}$ primibrachial width<br>$2^{nd}$ primibrachial height: $2^{nd}$ primibrachial width |
| *height versus width* | short / medium / long<br>uniserial / biserial<br>slender / robust<br>smooth / flat / ridged / grooved<br>fused / partially fused / coiled / cylindrical (Fig. 2c)<br>angle of arms (if fused)<br>linked by lateral processes |
| *cross-section* | cigar-shaped / triangular/trapezoid |
| **13. Arm branching** | |
| *type of branching* | isotomy / heterotomy / endotomy / exotomy / holotomy |
| *heterotomy* | description of main branch = ramus<br>smaller branches = armlets or ramules (ramuli) |
| *arm condition* | free arms on radials<br>proximal arms fixed, distal arms free<br>arm trunks |
| *brachial articulation* | fixed / free<br>synostosial / syzygial / synarthrial / trifascial synarthrial<br>transverse fulcral ridge<br>'zipper-like' structures |
| *pattern of brachials* | unknown / uniserial / biserial / cuneate / wedge-shaped |
| *interbrachials* | depressed / confluent with brachials |
| *secundibrach* | small / large<br>simple / axillary<br>nodose / spinose |
| *tertibrach* | small / large<br>simple / axillary<br>nodose / spinose |
| *quartibrach* | small / large<br>simple / axillary<br>nodose / spinose |

| | |
|---|---|
| *finials* | small / large<br>simple / axillary<br>nodose / spinose |
| **14. Axillaries** | equal / unequal<br>1 / 2 / 3 / 4 / 5 or more |
| *aboral sculpture* | smooth / spinose / wrinkled / ridged / granular fluted<br>pitted / nodose / pustulose<br>prominent / flared<br>upper distal sloping surface<br>notched by adoral groove<br>pierced by the axial canal<br>height versus width |
| **15. Pinnules** | absent / present<br>fixed / free<br>short / long<br>morphology homeomorphic / xenomorphic |
| **16. Pinnulars** | absent / unknown<br>short / long / slender / wide<br>equidimensional proximally<br>increasingly convex distally<br>elongate distally<br>tapering gradually to distal end<br>competent / feather-like / random<br>spines / hooks |
| *spacing* | wide / close-packing / overlapping |
| *proximal pinnulars* | convex transversely / specialised<br>inserted at right angles / obliquely |
| *cross-section* | set wide apart / overlapping / sub-triangular<br>laterally flattenened |
| *sculpture* | granular / spines / nodes / hooks / comb-like structures<br>longitudinal median keel<br>bifurcating / unbifurcated / uniserial |
| *insertion* | right angles / oblique<br>initially at right angles and then abruptly oblique |
| *folding* | inwards / interlocking |
| *distal pinnules* | tooth-like projections / paddle-shaped / prismatic / terminal comb |
| *symmetrical* | cylindrical / sub-cylindrical<br>elliptical U-shaped / interlocking |
| *asymmetrical* | folded inwards / interlocking<br>lateral adthecal side (side directed toward theca)<br>lateral abthecal side |
| **17. Column** | |
| *gross morphology* | absent / present / unknown<br>short / medium / long<br>slender / robust / massive<br>straight / twisted / planispirally coiled /curved / angular<br>homeomorphic / xenomorphic / heteromorphic<br>holomeric / bimeric / tetrameric / trimeric / pentameric |
| *xenomorphic* | gradual changes / abrupt changes in column between proxistele, mesistele and dististele |
| *proxistele* | homeomorphic / heteromorphic<br>short / medium / long<br>slender / robust / massively robust |

| | |
|---|---|
| | reduced proximal columnals just below crown (e.g., *Pisocrinus)*<br>enlarged proximal columnals (reducing flexibility, e.g., *Apiocrinites*)<br>enrolled proximal column hiding crown (e.g., *Ammonicrinus*) |
| *mesistele* | homeomorphic / heteromorphic<br>short / medium / long<br>slender / robust / massively robust<br>straight / twisted / planispirally coiled<br>non-flexible / flexible |
| *dististele* | homeomorphic / heteromorphic<br>short / medium / long<br>slender / robust / massively robust<br>straight / twisted / planispirally coiled<br>non-flexible / flexible |
| *horizontal X section*<br>*longitudinal X section* | circular / sub-circular / elliptical / square / pentagonal<br>description |
| *nodals* | unknown / absent / present |
| *internodes* | 1N / 2N / 3N / 4N / unknown |
| **18. Latera** | height, width |
| *shape* | sculptured / unsculptured<br>planar / concave / convex |
| *radice / cirrus scars* | absent / present<br>nodal / bimodal / compound |
| **19. Articular facets**<br>*outline* | <br>shape |
| *articulation* | synostosial / symplectial / cryptosymplectial / synarthry |
| *synartrial articulation* | fulcra aligned / non-aligned within columnals<br>circular with deep bifascial pits (e.g., bourgueticrinids)<br>fulcral ridges on alternate pairs of opposed facets rotated $180^0$ |
| *epifacets* | narrow / wide / thin / thick / taper<br>circular / square / triangular / pentagonal / hexagonal / polygonal / stellate / petaloid / patterned |
| *crenula* | absent / present (Fig. 2E, F) |
| *crenularium*<br><br><br><br>*crenellae* [grooves]<br><br>*culmina* [ridges] | narrow / wide<br>radiates continuously towards the axial canal<br>width:<br>narrow crenularium / wide areola / crenulate perilumen<br>shallow / deep<br>number<br>ridge and groove equal / subequal<br>ridge narrower than groove |
| *areola* | unknown / unseen<br>shape / size |
| *perilumen* | present / absent<br>width<br>smooth / sculptured / crenulate / ridged |
| **20. Lumen** | small / medium / large / gracile / robust |
| **21. Axial canal** | small / medium / large / narrow / broad<br>perforate / imperforate |
| *position* | centre / excentric |
| *shape* | circular / bluntly rounded<br>quinquelobate / subpentagonal / sharply pentagonal / pentastellate |
| *spatium* | shallow / deep<br>shape |

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|---|---|
| *jugulum* | absent /present<br>shape<br>circular transversely<br>jugulum extended by narrow slits radiating into septa to form a lineate star |
| *claustra* | absent / present<br>shallow / deep<br>clavate / pentastellate indentations |
| **22. Column appendages** | |
| | absent / present<br>slender / robust<br>branched / unbranched<br>aligned / non-aligned |
| *position* | along entire length of column / disistele only |
| *type of appendage* | radices / cirri |
| *radices* | absent / present<br>single / few / many<br>present in the proxistele / mesistele / disistele / present along entire length of column |
| *true cirri* | absent / present<br>jointed slender / very slender<br>straight / gently curved<br>maximum width<br>closely spaced / widely spaced<br>taper constantly / taper distally<br>cirral length<br>present: proxistele / mesistele / disistele<br>present along entire length of column<br>ossicles; circular / elliptical spatulate<br>weakly rhomboidal / strongly rhomboidal<br>number of ossicles<br>cirral latera smooth / sculptured<br>articulation<br>cirral central canal<br>terminal claw absent /present<br>opposing spine |
| *aligned whorls* | slender / elongate<br>complete / incomplete<br>occupying single site<br>occupying two or more sites at any node (compound)<br>semi-aligned / non-aligned |
| *cirrus scars* | width;<br>% of nodal diameter;<br>small / medium / large (defined by Simms, 1989: small = < 25 %, medium = 25 - 50 %, large = > 50 %)<br>aboral lip<br>weakly to strongly tuberculate |
| *cirral attachments:* | polynodal articulations<br>binodal articulations with fossae<br>grooved lumen trace<br>number of ossicles per cirrus<br>synostosial articulation<br>symplectial articulation |

| | | |
|---|---|---|
| | | synarthrial articulation: fulcral ridges / bifascial fields<br>zygosynostosial articulation<br>ankylosial articulation |
| | *occupying sites:* | node / compound nodes / overlapping onto internodals |
| | *radice /cirral lateral shape dimensions* | quadrangular / subequal |
| | *radice / cirral attachments* | equal / non-equal<br>grooved lumen trace |
| | *latera* | oval / lanceolate / lozenge-shaped / truncate –circular |
| | *axial canal* | minute / small / medium / large<br>shape |
| | *nudinodals* | lacking radices / cirri |
| **23.** | **Holdfast (apart from those with radices of cirri)** | |
| | *apparently lacking* | absent / unseen / unknown |
| | *hollow tube* | small irregular plates, e.g., *Aethocrinus* (hohlwurzel)<br>width |
| | *distal coils* | e.g. *Ctenocrinus pachydactylus* (Hess *et al*., 1999)<br>loose coils / tight coils |
| | *bulbous* | highly specialised chambered bodies e.g. scyphocrinitids<br>width |
| | *columnals* | circular / oval / wedge-shaped |
| **24.** | **Terminal holdfast (lacking well-defined radices)** (Fig. 3) | |
| | *discoidal* | pad-like structures<br>width |
| | *outline* | circular / conical |
| | *margins* | lobate / digitate / crater for stem attachment<br>simple / compound / multiplated<br>short / very short / long / very long |
| | *root attachment* | shell / hardground / soft substrate / other |
| **25.** | **Radicular holdfast** | |
| | *radicular* | none |
| | *radicular*<br>*radices* | tapers distally<br>at regular / irregular intervals |
| | *arrangement* | sparse / many<br>apparently on one side of columnal / radiating<br>short / very short / long / very long<br>slender / robust<br>radices clustered at distal end of column<br>circular in cross-section<br>branched / unbranched |
| | *radices united by* | symplexy / synostosis / ankylosis |
| **26.** | **Grapnel** | primary root system / no primary root (Fig. 3C) |
| | *radices* | absent / present<br>loboliths / crustose |
| **27.** | **Dististelar holdfasts (= stem segment holdfasts)**<br>**Tuberous** [distal end resembles radix (root)] | |
| | *branching radices* | bulb roots / stake-like |
| **28.** | **Rhizoidal** | clockwise / counterclockwise<br>small / large<br>stout / strong |
| **29.** | **Stoloniferous** | alignment of radices |
| | *stem* | pseudo-cirri / creeping roots / slender / long |
| | *heteromorphic* | long / tubercular / distal tapering / with axial canal |

| | | |
|---|---|---|
| | *branching* | jointed / unjointed |
| | *stereom extensions* | simple / jointed / nonjointed / distal tapering |
| | *distal coils* | knobs / rods / columnal flanges |
| | *coils* | jointed / unjointed / planar / tight / tapering / flattened |
| | *internodals* | tight / loose / wedge shaped |
| **30.** | **Additional observations and comments** | |
| | *ontogeny* | morphogenic character measurements (Meyer & Ausich, 1997) |
| | *behaviour* | (e.g., larval selection behaviour preference over one substrate or another) |
| | *physiology* | disease, parasitism, diets |
| | *evidence of regeneration* | |
| | *spacing, community, relative abundance* | |
| | *data and evidence for determining stenotopy to eurytopy spectrum* | |
| | *other useful comments* | |

In his inspiring Annual Address to the Palaeontological Association, Boucot (2006) considered the question of what can be included in taxonomic descriptions. He advocated expansion of routine taxonomic description, explaining that 'organisms are far more than their basic morphology.' His suggestions included documenting evidence and informed inference of ontogeny, behaviour (e.g., behaviour preference of larvae over one substrate or another), spacing, physiology, disease, parasitism, diets, community, data concerning stenotopy or eurytopy, relative abundance and any other useful comments. Boucot emphasised the importance of including discussions of ontogeny and looking for ancestral stocks. Essentially, he favoured adding all detailed information which would enable clearer and better understanding of taxa, thus furthering the science. Table 2 includes some of Boucot's suggestions.

In the current paper, I attempt to define the principal morphological components that need to be discussed in a description of a fossil crinoid. The structure of the paper broadly follows that of Lewis & Donovan (2007), who published an analogous methodology for describing fossil echinoids. Herein, I present an ordered checklist of the principal features of the crinoid endoskeleton that should be examined and determined in all descriptions (Table 1). The range of morphologies of fossil crinoids is large, and further, more comprehensive discussion and definition of terms can be found in Moore & Plummer (1940), Moore *et al.* (1968, 1978a) and Ubaghs (1978), amongst others.

Terminology of the crinoid crown, theca, aboral cup, aboral cup, tegmen and calyx is commonly misused or at best confused (W.I. Ausich, written comm.). Likewise, the terms ramules, armlets and pinnules are ill-used (Webster & Maples, 2006). The following distinctions are important to note and are mainly derived from the glossary of descriptive terms in Moore & Plummer (1940, pp. 17-22).

Firstly, the terms 'aboral cup,' 'dorsal cup' and 'cup' are interchangeable and relate to the part of the crinoid from the radials to the top of the columnal (stem). The calyx represents those hard parts of a crinoid exclusive of the arms and the stem; that is, the aboral cup, tegmen and anal series. The crown is the crinoid without the stem (calyx plus arms). The tegmen (otherwise called ventral disc, vault dome or summit) is the cover above the aboral cup, inside the bases of the free arms. The anal X is the lowest tube plate of the anal series. 'Orals' are five plates in interradial position that cover the mouth. The terms 'anal sac,' 'anal tube' or 'ventral sac' (usually rounded or tubular) are used for an outgrowth from the tegmen of a crinoid, enclosing part of the gut and carrying the anal vent at its apex or on the side. 'Rami' are individual branches of an arm or ray and refer to arms that branch only once. Finally; 'pinnules' are probably best thought of as the ultimate production of arm division.

Webster & Maples (2006) emphasized the importance of anal plates for crinoid classification and, in addition, suggested detailed descriptions of radial facet surface morphology for use in lineage, classification and palaeoenvironmental applications.

The fossil crinoid checklist has been designed to aid the writing of descriptions, and promote a systematic approach which will encourage and facilitate the study of crinoids, a major invertebrate group with a complex morphology due to their multiple skeletal elements. Table 2 has been adapted from Lewis & Donovan (2007) as a quick reference guide to ensure that all essential and relevant details are recorded to assist present and future researchers viewing specimens in museum collection(s). Figures 1-3 clarify some of the morphological features/descriptors necessary in describing crinoids. The systematic section provides an example of the use of the checklist. It is anticipated that this checklist will provide a useful tool on which to build and will help to avoid confusion arising from inconsistencies between descriptions.

Whilst it is important to describe in detail all aspects of the crinoid, it is perhaps worth mentioning that, traditionally, classification of crinoids has focused on the

Table 2. Checklist to assist crinoid descriptions (modified after Lewis & Donovan, 2007).

| | | |
|---|---|---|
| *Details 1* | | |
| **Diagnosis** | Short, concise sentences summarising essential characteristics of genus or species | |
| **Etymology** | Background to name / help with pronunciation | |
| **Material** | All specimens listed<br>• holotype<br>• paratype(s)<br>• syntype(s)<br>• lectotype<br>• neotype(s)<br>• other material | Museum(s) or other repository where the specimens are stored; registration number of specimen(s); name of collector / collection and other details where appropriate. |
| | Preservation of the specimen(s) | |
| **Localities** | In ascending order, e.g., above the bentonite, Wether Law Linn Formation, North Esk Inlier, Pentland Hills, Midlothian, Scotland. Locality R82 of Robertson (1985) | |
| **Stratigraphy** | chronostratigraphy<br>biostratigraphy<br>lithostratigraphy | |
| *Details 2* | | |
| **Gross morphology;** size / shape | | |
| **Morphological description of taxon** | | |
| **Plates, figures and tables** | | |
| **Additional observations** | | |
| **Comparisons / Discussion;** ontogeny, behaviour, physiology, *etc.* | | |
| **Conclusions** | | |
| **Acknowledgements** | | |
| **References** | | |

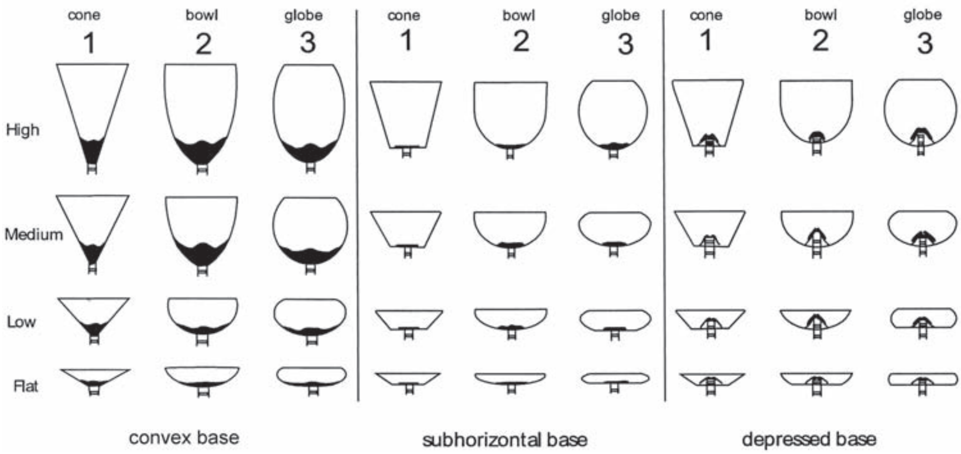


Fig. 1. Variation in shape of the calyx in crinoids (redrawn after Ubaghs, 1978, fig. 72).

crowns. It is important to emphasize that disarticulated stems can be useful and are often found in abundance where complete crinoid specimens are not (Moore *et al*., 1968; Donovan, 1986, pp. 13-18).

## Methodology

Observations and measurements were made of all specimens of a new collection of *Pisocrinus* cf. *campana* S.A. Miller, 1891, from a new locality using a Wild binocular microscope and a scanning electron microscope (SEM), Jeol JSM 6480LV. All the specimens were preserved as natural external moulds and required casting with latex rubber using standard techniques (Feldmann *et al*., 1989).

Terminology of the crinoid endoskeleton follows Brett (1981), Hess *et al.* (1999), Moore & Plummer (1940), Moore *et al.* (1968, 1978a), Ubaghs (1978) and Webster (1974). The term 'radices' has been used rather than 'radicular cirri' (Donovan, 1993). The term 'cirri' is used for jointed attachments of (mainly) isocrinines and comatulids.

## Systematic palaeontology

### Class Crinoidea J.S. Miller, 1821
### Subclass Disparida Moore & Laudon, 1943
### Family Pisocrinidae Angelin, 1878
### Genus *Pisocrinus* de Koninck, 1858a

*Type species* – *Pisocrinus pilula* de Koninck, 1858a, p. 104, by monotypy (Moore *et al.*, 1978b, p. T534). For an English translation, see de Koninck (1858b).

*Diagnosis* – (After Moore *et al.* 1978b, pp. T534–T535.) "Cup small, globose or rarely conical with flat base or basal concavity; basals 5, unequal in size, *AE* and *BC* basals smaller than other 3 basals and with truncated rather than acute distal edge. Radials

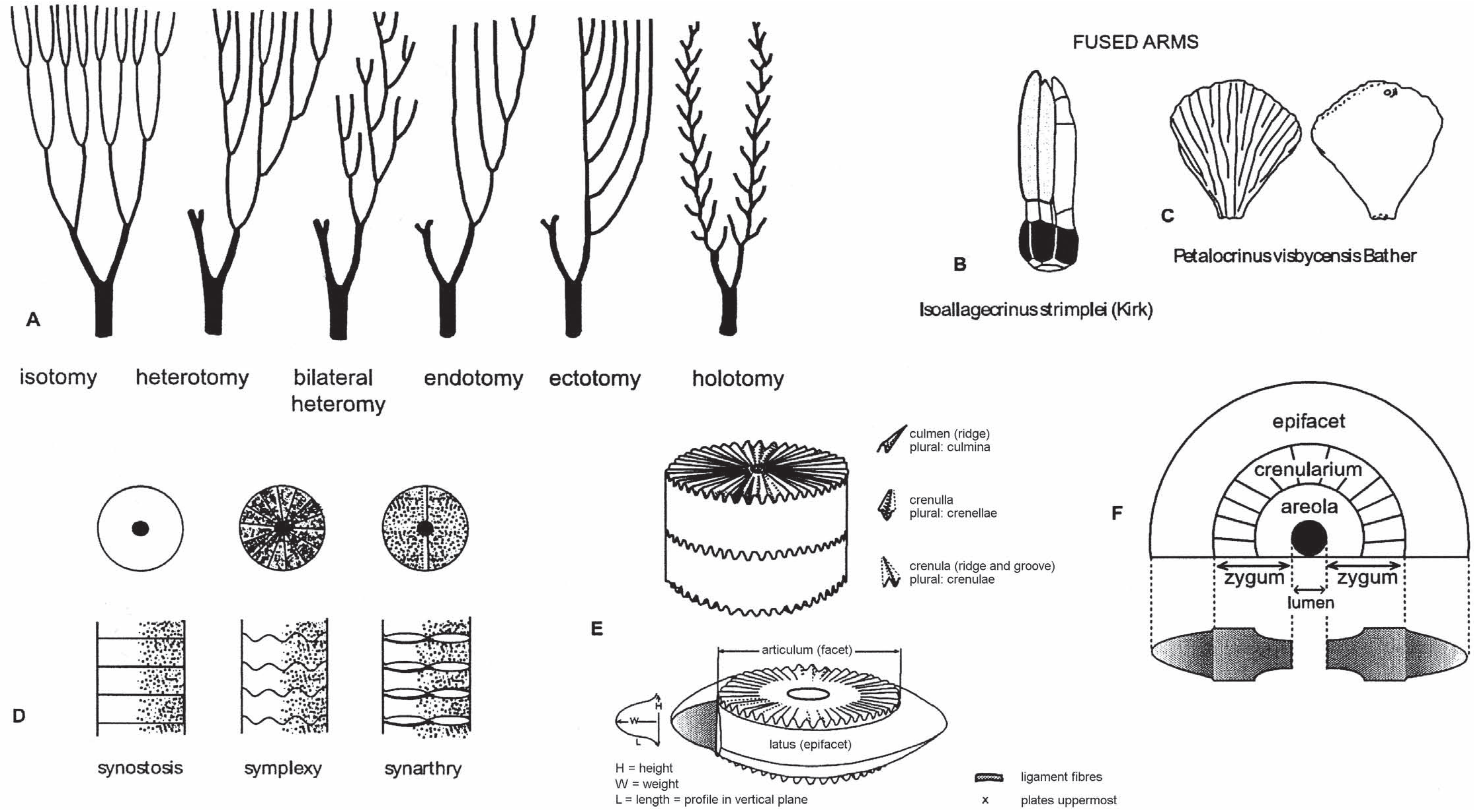


Fig. 2. Features of crinoid arms and stems. (A) Principal patterns of arm branching (redrawn after Ubaghs, 1978, fig. 115). (B, C) Crinoids with fused arms. (B) Crown of *Kallimorphocrinus strimplei* (Kirk) (redrawn after Ubaghs, 1978, fig. 124.1). (C) Adoral (left) and aboral (right) surfaces of fused arms of *Petalocrinus visbycensis* Bather. (D) The three principle geometries of articulation in the crinoid stem (redrawn after Donovan, 1989, fig.1) (E). Some morphological features of crinoid columnals with symplectial articulation (redrawn after Moore *et al.*, 1968, fig. 2). (F) Partial articular facet of columnal and median longitudinal section of same (modified after Moore *et al.*, 1968, figs. 1, 2).

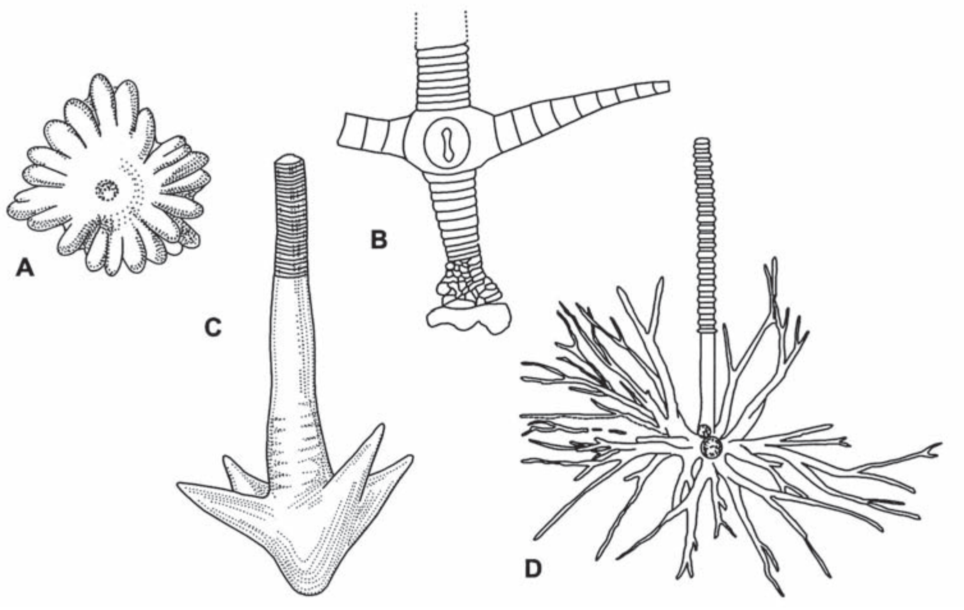


Fig. 3. Examples of morphological diversity in Palaeozoic crinoid attachment structures (redrawn after Ubaghs, 1978, fig. 64. 5, 66.1, 66.3, 66.4, respectively). (A) *Aspidocrinus digitatus* Hall, cemented discoidal attachment. (B, C) *Ancyrocrinus bulbosus* Hall. (B) Immature specimen. (C) Mature grapnel attachment. (D) *Eucalyptocrinites ovalis* (Hall), distal radicular holdfast.

unequal in size, *C* and *E* radials small, triangular and not in contact with basals; *B* ray with small triangular superradial and large inferradial which is shifted obliquely to the left and situated directly above the *BC* basal; the *D* and *A* radials are large, simple, in contact with basals, and together with the *B* inferradial comprise most of the theca. Anal *X* small, situated above cup and in contact with upper corners of *C* and *D* radials. Arm facets deeply notched into upper surfaces of radials; articular surfaces with fine radial ridges and grooves, or a transverse ridge; facets bounded laterally and internally by raised outer edges of the radials. First primibrachial short, remainder of brachials slender and elongate; arms atomous and nonpinnulate. Anal sac narrow and elongate, closely resembling an arm, triangular or crescentic in cross section, supported directly by anal *X* and confined to the posterior part of the tegmen. Tegmen arched by 5 oral plates which interlock medially and are in sutural cotact with the radial processes."

*Range* – Lower Silurian – Lower Devonian (Webster, 2003).

***Pisocrinus* cf. *campana* S.A. Miller, 1891**
Pls. 1, 2.

cf. 1891 *Pisocrinus campana,* S.A Miller, p. 32, pl. 11, figs. 4, 5.
cf. 1892 *Pisocrinus campana* Miller; S.A. Miller, p. 642, pl. 11, figs. 4, 5.
cf. 1897 *Pisocrinus* sp.; Wachsmuth & Springer, pl. 8, fig. 10.
cf. 1915 *Pisocrinus campana* Miller; Bassler, p. 980.

cf. 1926 *Pisocrinus campana* Miller; Springer, p. 76, pl. 24, figs. 6-27.
cf. 1943 *Pisocrinus campana* Miller; Bassler & Moodey, p. 612.
1952 *Pisocrinus* cf. *campana* Miller; Lamont, p. 29.
cf. 1975 *Pisocrinus campana* Miller; Brower, p. 637, pl. 74, figs. 1, 2,
cf. 2007 *Pisocrinus campana* Miller; Donovan *et al*., pp. 176, 178, pl. 34, figs. 3, 4.
cf. 2008a *Pisocrinus campana* Miller; Donovan *et al*., table 16.1.
2008b *Pisocrinus* cf. *campana* Miller; Donovan *et al*.

*Material studied* – All specimens deposited in the Nationaal Natuurhistorisch Museum, Leiden, RGM 542 914-542 982 (68 specimens). Specimens are all preserved as external moulds and are well preserved, enabling casting by latex. Cups are preserved in a number of different orientations. Most parts of the crinoid are preserved although no single specimen is complete. The similarities of these specimens to *P. campana* are discussed in detail by Brower (1975).

*Locality and horizon* – Silurian; Llandovery; Telychian; Wether Law Linn Formation; lower member; above the Bentonite of locality R82 of Robertson (1985, 1989), in the North Esk Inlier, Pentland Hills, Midlothian, Scotland. This is not the locality R265 of Clarkson *et al*. (2007), mentioned by Lamont (1952) and Brower (1975).

*Description* – Crown slender and elongate. The aboral cup is small, medium bowl shaped to globose. The sides are convex and height is approximately equal to width (Pl. 1, fig. 3) or forming a medium cone (Pl. 1, fig. 6). The sides are medium to high, fairly straight with interradial concavities and radial convexities immediately below the radial (arm) facet (Pl. 1, figs. 6, 7). Aboral cup circular to pentolobate in plan view. Relative to the base of the cup, the column is wide with a distinct proxistele. Base of cup truncated and slightly depressed. Cup plates smooth, sutures between plates difficult to distinguish. Basals and basal circlet indeterminate. Radials apparently large, but indistinguishable from each other. Radial facets are triangular with a deep notch. Radial processes lanceolate to cuboid. Tegmen not preserved, anal series unseen.

Primibrachials upflared. Five free arms, short to long, unbranched, apinnulate, equal to subequal in size, triangular to cigar-shaped in cross-section and with a smooth sculpture. Arms may be long and slender or short and robust. Brachial articulation with the radial broad; $IBr_3$ is the most distal brachial seen. Arms taper gradually distally. Sides of adoral surface of brachials show slight 'zipper-like' indentations.

Articulation between calyx and proxistele apparently symplectial. Axial canal moderately broad, central, subcircular. Xenomorphic stem with proxistele, mesistele and dististele (=holdfast). Column circular in section. Proxistele has approximately ten low columnals followed by more stout, barrel-shaped columnals of homeomorphic mesistele. RGM 542 917 (Pl. 2. fig. 3) is interpreted as a mesistele trending into the dististele and showing two attached slender radices emerging from nodals. Holdfast distal, radicular. RGM 542 917 showing radicular holdfast with barrel-shaped stem and bearing four radices at angles of between 100° - 135° to the more anterior column, the most complete of which branches dichotomously.

*Representative measurements (in mm)* –Abbreviations follow Donovan & Paul (1985, text-fig. 1; Fig. 4 herein): maximum diameter = D; diameter of oral surface = $D_{oral}$; diameter of base of cup = $D_{base}$; articular facet diameter = FD (cf. Moore *et al.*, 1968); total height = H; height at maximum width = $H_{Dmax}$.

| Specimen | D | $D_{oral}$ | $D_{base}$ | FD | H | $H_{Dmax}$ |
|---|---|---|---|---|---|---|
| RGM 542 915 | 2.8 | 0.8 | 1.8 | 0.8 | 2.8 | 2.2 |
| RGM 542 916 | 1.9 | 1.5 | 0.6 | – | 1.7 | 1.7 |
| RGM 542 917 | 3.7 | 0.8 | 0.6 | – | 1.7 | 1.5 |
| RGM 542 923 | 2.00 | 1.6 | – | 0.8 | 2.3 | 1.7 |

*Additional observations* – *Pisocrinus* cf. *campana* are the only crinoids found at this location and are relatively abundant. Preservation of such well preserved, small, delicate structures strongly suggests they were buried in some sort of an obrution deposit. The variation in gross morphology of the cup poses the question as to whether these different forms could represent either stages in ontogeny, (sexual?) dimorphism or both. Although the possibility of changes during ontogeny cannot be ruled out, cup shape variation also suggests that different species may have co-existed in an environment where overcrowding was not a factor. Measurements useful for such an analysis are suggested in Table 3.

*Remarks* – The classification of pisocrinids is problematic due to their simple morphology. Even in extant crinoids, it may be difficult to tell if similar forms represent different taxa or are merely variants within species (Messing, 1997). Crinoids may develop differently under different flow regimes; however, the specimens described herein, all collected from a single locality, are more likely to be different due to variation

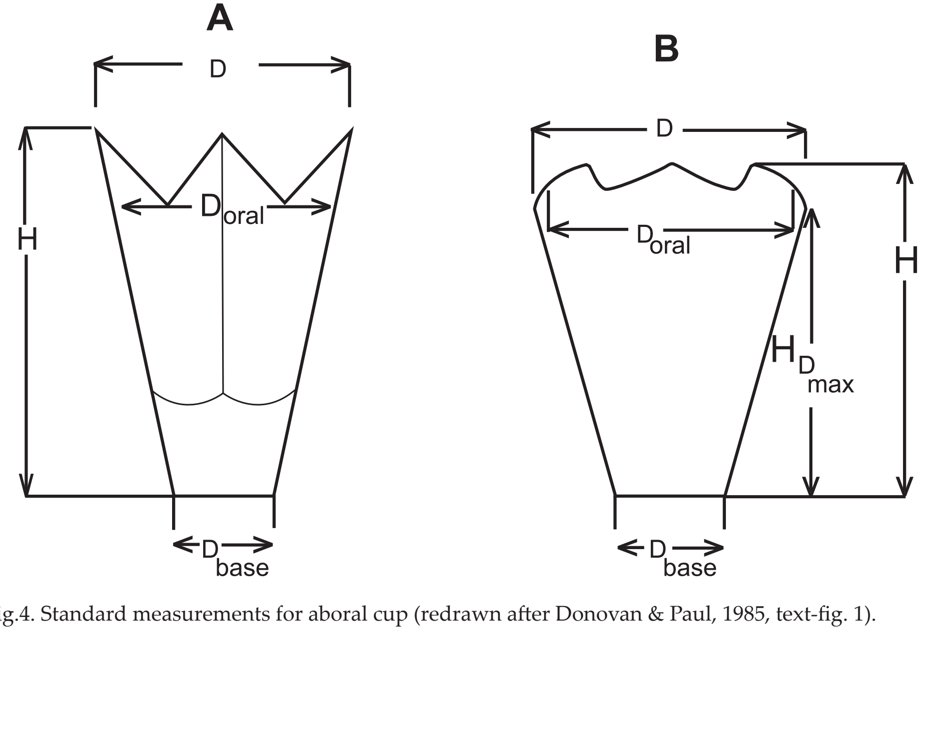


Fig.4. Standard measurements for aboral cup (redrawn after Donovan & Paul, 1985, text-fig. 1).

Table 3. Characters that may usefully be measured to establish ontogentic variation (adapted after Meyer & Ausich, 1997). For more detailed information regarding measurements of the stem, see Moore *et al*. (1968).

| | |
|---|---|
| *calyx measurements* | height |
| | calyx diameter through A ray to CD interray |
| | radius of CD interray |
| | radius of C ray |
| | radius of A ray |
| | radius of AB interray |
| *brachial measurements* | 1$^{st}$ primibrach height |
| | 1$^{st}$ primibrach width |
| | 2$^{nd}$ primibrach height |
| | 2$^{nd}$ primibrach width |
| | 1$^{st}$ interbrachial height |
| | 1$^{st}$ interbrachial width |
| | arm facet height |
| | arm facet width |
| *columnal measurements* | diameter of proximal columnal(s) |
| | diameter of lumen [expression of axial canal across facet] |
| | KH columnal height |
| | KD columnal diameter |
| | LD lumen diameter |
| | FD facet diameter |

during ontogeny. Low diversity of other taxa from this locality (Robertson, 1985, 1989) might suggest all the pisocrinids are variants of one species. Because *P*. cf. *campana* is the most abundant, this may indicate that the local environment particularly suited their ecological requirements. In consequence, I have documented the specimens as a single species until further data are made available.

Pisocrinid specimens from the same location have shown variation in form, particularly in the dimensions and shape of the calyx. The variations could represent different taxa, but the possibility of ontogeny or even dimorphism cannot be ruled out. Short-armed species such as *Pisocrinus quinquelobus* exhibit spear-shaped radial processes and long-armed species *Pisocrinus campana* have square-shaped processes, representing two adaptive strategies for strong, protecting posture (Ausich, 1977). Both morphologies are present in this assemblage, for example, RGM 542 922, 542 923 and 542 915 (Pl. 1, figs. 3, 5, 10, respectively).

Webster (2003) recognised about 30 valid nominal species of *Pisocrinus.* Springer (1926) noted the problem of recognising the limits to species in *Pisocrinus* and speculated that, from a list of eleven species which he considered, at least some of them may have been synonymous. Springer's Collection, now in the National Museum of Natural History, Smithsonian Institution, contains a large number of specimens of *P. campana,* which is most commonly found in the lower half of the Brownsport Formation, but ranges throughout this unit (Amsden, 1949).

The type locality for *Pisocrinus campana sensu stricto* is Upper Llandovery or Wenlock, Salamonie Dolomite, Wabash, Indiana, U.S.A. Other American localities include; Upper Llandovery, Osgood Formation, St. Paul and adjacent areas in southern Indiana;

Lower Wenlock, Laurel Limestone, St. Paul, Indiana; and Lower Ludlow, Brownsport Formation, various localities in Wayne, Perry and Decatur counties, Tennessee (Brower, 1975). Springer (1926) cited dolomites of Wabash, Marion, Anderson, northern Indiana; Osgood and Laurel; St. Paul and other localities in southern Indiana; Laurel and Brownsport formations. Rise Mill and Flatwoods, Perry County; Martin's Mill, Sinking Creek, Wayne County; Tuck's Mill and various glades in Decatur County, Tennessee.

Morphological structures of the cup include concavities and convexities, as described above, directly correlated to the position of the arms. Slight convex swellings occur immediately below radial facets and are interpreted herein as possible structural supports. The zipper-like structures on the edges of the blade-like arms could have been used for holding the arms together against strong currents (Ausich, 1977), analogous to extant *Holopus rangii* d'Orbigny (Donovan, 1992). During arm enrollment, the adjacent arms of *H. rangii* abut and form an impervious seal (Grimmer & Holland, 1990). Presumably, the 'zipper-like' structures in the pisocrinids served a similar function. It is necessary for the more distal brachials of *H. rangii* to be narrow and V-shaped to permit enrollment (Donovan, 1992); analogously, the more proximal brachials of *P*. cf. *campana* must have been broad to permit abutment with adjacent arms. Whilst the pisocrinids here described were not expected to have been able to enrol their arms, it is assumed that they would have been able to close them effectively and, therefore, potentially could withstand a moderately high energy environment. When arms were closed together, the slim profile of the crinoid would have created little resistance in the water flow. Presumably the barrel-shape of the columnals would have disrupted the water flow slightly.

Some specimens appear shorter because only $IBr_1$ is preserved. In *H. rangii,* the absence of easily identifiable plate sutures acted to strengthen the calyx (cf. Donovan, 2006, p. 399). The smooth pisocrinid cup with its near-indistinguishable sutures may similarly have been strengthened against environmental forces such as currents and perhaps also mitigated against boring infestation.

Preservation in a fine-grained sandstone suggests a low to medium energy environment for this particular horizon and the Lower Member of the Wether Law Linn Formation has been interpreted as a shallow marine barrier complex (Robertson, 1989, p. 138). The taphonomic spectrum of preservation is as follows: some specimens are articulated and almost complete; some cups are detached from their columns; some bladed arms are detached, but are close to their cups; and numerous arm blades are preserved in the rocks as single entities.

The morphology of the column suggests some flexibility proximally with low columnals acting similarly to 'bendy straws' (compare with Donovan, 1984, p. 831), whereas the stouter 'barrel-shaped' columnals of the mesistele and dististele were relatively taller and less flexible. Available specimens suggest that the holdfast was a gently tapering stem with two or more unbranched(?) radices.

*Conclusions* – The re-description of *P.* cf. *campana* is an example of how the fossil crinoid checklist can be a useful tool. Systematic, detailed descriptions will make taxonomic comparisons easier and more objective. It will also encourage us to carefully note and distinguish between what is absent, unseen, unknown and/or not preserved, which may be as important as what is present.

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Professor Stephen K. Donovan (Nationaal Natuurhistorisch Museum, Leiden) and Mr. David N. Lewis (The Natural History Museum, London) encouraged me to create this checklist, and allowed me access to their joint paper before it was published. Steve provided financial support for my fieldwork in Scotland. I thank my supervisor, Dr. Charlie J. Underwood (Birkbeck College, University of London), for his continued support and Professor Euan N.K. Clarkson (University of Edinburgh) for arranging fieldwork in the Pentland Hills. Mr. Kees van den Berg and Dr. Lars W. van den Hoek Ostende (both Nationaal Natuurhistorisch Museum, Leiden) provided instruction in the use of the SEM, as well as support and encouragement. I am grateful for the constructive review comments from Professor Wiliam I. Ausich (The Ohio State University, Columbus), Professor George Sevastopulo (Trinity College, London) and Mr. Dave Lewis.

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**Plate 1**

*Pisocrinus* cf. *campana* S.A. Miller, 1891

Fig. 1. RGM 542 936, aboral cup, lateral view. Scale bar represents 200 μm.
Fig. 2. RGM 542 917, aboral cup, partly disarticulated. Large plate on left probably D radial supporting small E and C, BC inferradial to right, small anal X(?) upper right, but displaced (for comparison, see Ausich, 1977, p. 673; Brower, 1975, p. 648). Scale bar represents 500 μm.
Fig. 3. RGM 542 922, showing aboral cup in lateral view with arms retaining some first primibrachials. × 15.
Fig. 4. RGM 542 915a, oblique basal view of aboral cup showing depressed articular facet of the base of the cup and plating with associated pluricolumnals. Large radial on right interpreted as inferradial and left radial therefore D. Cup 2.8 mm high (p. 53).
Fig. 5. RGM 542 923, dorsal cup, lateral view showing square radial process (compare to long-armed specimens of *P. campana* in Ausich, 1977, fig. 6B). Scale bar represents 500 μm.
Figs. 6, 7. RGM 542 920. a, b, part and counterpart showing crown, proxistele and mesistele. Scale bar represents 1 mm.
Fig. 8. RGM 542 918, crown with proxistele attached, complete arms slightly disarticulated from cup. × 4.4.
Fig. 9. RGM 542 915a, aboral cup, arm and proxistele with part of proximal stem. × 6.
Fig. 10. RGM 542 915b, aboral cup with disarticulated column. Lateral view showing spear-shaped radial process (short-armed specimen *sensu* Ausich, 1977, fig.6A). × 14.

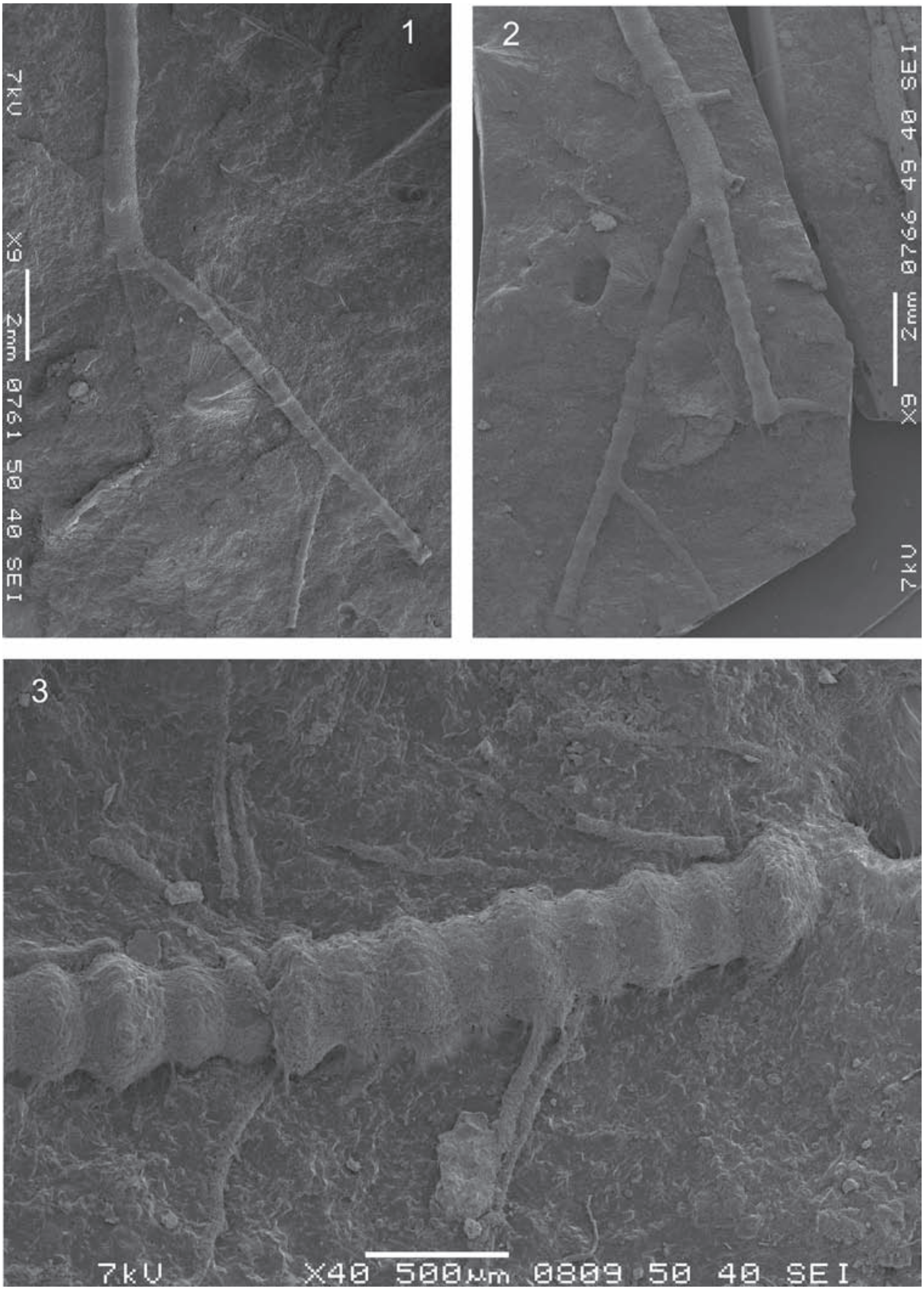
Scanning electron micrographs of latex casts taken from natural external moulds. Casts coated with gold.


1
X65 200µm 0335 21 49 SE
2
X45 500µm 0798 20 40 SEI
7kU
3
4
5
X40 500µm 0345 22 49
6
7
X20 1mm 0612 19 68 SEI
3.0kU
8
9
10

**Plate 2**

*Pisocrinus* cf. *campana* S.A. Miller, 1891
Figs. 1, 2. RGM 542 914 a, b, part and counterpart, attachment structure, distal radicular holdfast. Scale bars represent 2 mm.
Fig. 3. RGM 542 917, pluricolumnal bearing radices. Scale bar represents 500 μm.

Scanning electron micrographs of latex casts taken from natural external moulds. Casts coated with gold.


1
7kV X9 2mm 0761 50 40 SEI
2
X9 2mm 0766 49 40 SEI
7kV
3
7kV X40 500µm 0809 50 40 SEI