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South America's earliest (Ordovician, Floian) crinoids

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Abstract.—Two new Early Ordovician crinoids have been discovered in Gondwanan rocks of northwest Argentina. *Ramseyocrinus argentinus* n. sp., among the most complete for the genus, aids in reconstructing key morphology. *Ramseyocrinus* is unorthodox with just four radials forming the entire cup, these articulating to five arms above and a tetrameric stem below. Evidence is presented radials comprise A, B, D, and E ray elements (C absent) with B and D radials adjoining to form a compound facet for the C arm. Thus the cup entirely lacks posterior plating; an elongate anal sac projects from the CD tegmen region alongside the C arm. Cup synapomorphies closely link *Ramseyocrinus* and the Middle Ordovician *Tetragonocrinus*; inclusion of this clade within disparids is tenuous. *Quechuacrinus ticsa* n. gen. and sp., increases the paleogeographic range of reteocrinid camerates, previously documented only from Laurentia. This taxon expresses synapomorphies characterizing the Late Ordovician *Reteocrinus*, demonstrating the antiquity of this morphotype.

Introduction

Fewer than two dozen Early Ordovician crinoid species have been described in contrast to hundreds of later Ordovician taxa. The record is largely Laurentian, with few Gondwanan taxa from Europe, North Africa, and the Arabian Peninsula. *Quechuacrinus ticsa* n. gen. and sp. and *Ramseyocrinus argentinus* n. sp., described here, occur in the Floian (late Early Ordovician) siliciclastic sequence of Argentina's northwestern Jujuy Province. They represent the earliest crinoids yet known from South America, extending the range of Gondwanan occurrences. *Ramseyocrinus* is a relatively poorly known and controversial taxon and all material was examined and key specimens re-illustrated for this study.

Geologic context

Extensive outcrops of largely shallow-marine, siliciclastic successions of the Argentine Cordillera Oriental are included in the Santa Victoria Group that encompass the Cambro-Ordovician Santa Rosita (Furongian-Tremadocian) and Acoite (Floian) formations (Bahlburg and Furlong, 1996; Astini, 2008). The crinoids described herein occur in the middle-upper part of the Acoite Formation, exposed at the Quebrada Los Baños, a tributary of the Quebrada Chamarra, Los Colorados area (23°34" S, 65°42" W), 30 km northwest of Purmamarca village, at the western foot of the Argentine Cordillera Oriental (Tumbaya Department, Jujuy Province).

The Acoite Formation reaches a thickness of ~2000 m in the Quebrada Chamarra and is interpreted as a shallow-marine succession displaying stacked, large-scale shallowing-upward cycles, encompassing shelf to shoreface settings (Astini and Waisfeld, 1993; Astini et al., 2004). The unit is biostratigraphically constrained within the *Tetragraptus phyllograptoides* (lower Floian) and the *Dydimograptellus bifidus* (upper Floian) graptolite zones (Toro, 1997; Toro and Maletz, 2008). The new crinoids described herein are found in the lower part of the *Dydimograptellus bifidus* Zone (lowermost upper Floian).

The new crinoids occur in a 50-cm thick, fossiliferous, yellow-green shale bed. This and other shales alternate with fine to very fine-grained sandstone intervals that display hummocky cross-stratified beds below and climbing ripple cross-lamination above. Quiet-water, background suspension ("fall-out") mud deposition, punctuated by oscillatory flows related to numerous storms and accompanying influx of coarser sediments, is indicated. A diverse trilobite fauna is also in the crinoid-bearing shales (Waisfeld and Vaccari, 2003).

Biogeographic context

An extensive Floian trilobite fauna reveals a complex biogeographic pattern, consistent with the South American margin at intermediate latitudes (McCormick and Fortey, 1999; Fortey and Cocks 2003; Benedetto et al. 2009). Endemism supports semi-isolation where provincially significant elements exhibit a mixture of affinities either with warm water areas or with cooler western Gondwana (cf. Waisfeld and Vaccari, 2008). Likewise, *Ramseyocrinus* occurs in cool water Gondwanan settings, whereas *Quechuacrinus* is judged phylogenetically close to the warm water Laurentian *Reteocrinus*.

Phylogenetic position of *Quechuacrinus*

The cup of *Quechuacrinus* is characterized by prominent truss-like plate ridges with fenestra or deep pockets at plate corners, similar to the Middle and Late Ordovician *Reteocrinus*.

The posterior morphology of *Reteocrinus* includes a prominent sagittal anal series of arm-like plates bisecting the CD interray, and extending from a basal plate. There is no articulation to ray plating. The posterior morphology of *Quechuacrinus* is incompletely known, but similar to *Reteocrinus* in expression of a prominent anal series, but not sagittal, instead articulating to the C-ray first primibrachial (Figs. 1, 2). Posterior plating more closely associated with the C-ray occurs in the early Floian putative reteocrinid *Cnemacrinus*, where the anal series extends from the basal below and C-radial. Pocket/fenestra expression in *Quechuacrinus* falls between *Reteocrinus* and *Cnemacrinus*.

Reteocrinus rocktonensis Kolata, 1975, has a sagittal anal series articulating to the C-radial rather than the first primibrachial. Its anal series is narrower than arms. The taxonomic status of this form is unresolved.

Crown construction and phylogenetic position of *Ramseyocrinus*

Much has been written about *Ramseyocrinus* (see Donovan and Savill, 1988; Donovan, 1989) and for a time, this taxon was recognized as the oldest known crinoid, influencing thinking on early crinoid phylogeny and origin of the class itself. However, *Ramseyocrinus* has historically been difficult to decipher, with differing views of cup homologies and crown orientation (Donovan, 1984, 1989; Cope, 1988). Six different interpretations are summarized in Donovan (1989, fig. 1).

Earlier authors (Bates, 1968; Ubaghs, 1983; Cope 1988) considered the four-plate cup base circlet of *Ramseyocrinus* to be basals. Donovan (1984; 1989) argued that these constitute radials, observing that cup base plates express prominent articular arm facets, so the articulating but not fixed plates above are first primibrachials. These putative primibrachs form in continuity with, and are similar to, subsequent primibrachs.

The radials of *Ramseyocrinus* are arranged in a rare pattern (Donovan, 1984, fig. 6). Uniquely, two cup plates support an arm and half of another appendage by sharing the arm facet. This is here termed a compound radial facet. The remaining two radials underlie and align with arms above in the normal arrangement. The four radials arrangement echoes the tetrameric stem of *Ramseyocrinus*, though not the symmetry.

Initially, the "co-supported" appendage of *Ramseyocrinus* was interpreted as an anal "tube" (Bates, 1968; Ubaghs, 1983; Donovan, 1984), but later, after discovery of a specimen demonstrating isotomous branching, as an arm (Cope, 1988; Donovan, 1989). The cup lacks any obvious posterior plating, and orientation was considered uncertain (Donovan, 1989, fig. 1.6).

Two pieces of evidence indicate the co-supported appendage is the C arm. First, it is bisected by the only symmetry plane in the cup (Fig. 3.4, 3.5), arguably the crinoidal plane. The cup of *Ramseyocrinus* expresses near perfect bilateral symmetry, with one large and one small plate per side. The cup CD interray is normally bisected by the crinoidal plane, but in this case, there is no CD interray. Second, the *R. argentinus* holotype preserves the lower portion of an anal sac curving and extending upward alongside the putative C ray arm (Fig. 4.4). We assume, then, the sac originates from the CD region of the tegmen. Previous authors illustrate disarticulated sac platelets associated with the putative C ray (this interpretation) of *R. vizcainoi* (Ubaghs, 1983, text fig. 11; fig. 3.2) and *R. cambriensis* (Cope, 1988, text-figs. 2b, 3; fig. 5.4), documenting this expression across all known *Ramseyocrinus* species. The anal sac extends to at least 80% of the total crown height of *R. cambriensis* (Fig. 6.4)

Identification of the C ray helps clarify the cup plate homologies of *Ramseyocrinus*. The unusual co-shared C radial facet supports the interpretation of no posterior cup plating or C radial; that functional role filled by expanded B and D radials.

Like *Ramseyocrinus*, the cup of *Tetragonocrinus* is built of just four plates with no anal plating; similar to, though not symmetrically disposed like *Ramseyocrinus* (Rozhnov, 1988, Fig. 1). This single cup circlet has been considered basals (Rozhnov, 1988), but extending the example from *Ramseyocrinus*, an alternative hypothesis posits radials. Synapomorphies include tetrameric stems and compound radial facets co-formed by adjacent radials, and lack of posterior plating. *Tetragonocrinus* expresses just three arms. Disparid ontogeny indicates A and D arms develop last (Sevastopulo and Lane, 1988; see also Rozhnov, 1988). Following this reasoning, these arms are absent in *Tetragonocrinus*.

The phylogenetic position of a putative *Ramseyocrinus*-*Tetragonocrinus* clade is cloudy. Close association of the anal sac and C arm suggests disparids or camerates. Few plated cup construction suggests the former.

The lower Silurian camerate *Stipatocrinus* Eckert and Brett 1987, expresses a similar cup base circlet pattern to that of *Ramseyocrinus*, but this similarity is interpreted as homoplastic. Here the cup base is formed by either infrabasals (following the DRHS of Guensburg and Sprinkle, 2003) or basals (by the "Treatise," Ubaghs, 1978).

Implications for the early radiation of crinoids

Taking a broad view, the new discoveries help document the great range of evolutionary tinkering with early diversification. This is apparent despite the relatively poor Floian crinoid record. These are not variations on a narrow theme, instead the range of morphologies points to differing adaptive strategies. The "minimalist" cup construction (single circlet, no posterior plating) in *Ramseyocrinus* contrasts sharply with coeval camerates (e.g. *Proexenocrinus*) and cladids (e. g. *Elpasocrinus*) with "usual" configurations and many more elements (see also Deline and Ausich, 2011).

Systematic paleontology

Terminology used here adopts both the Dual Reference Homology System following Guensburg and Sprinkle (2003) and Guensburg (2012), a modification of the Ubaghs (1978) terminology in the "Treatise." Repositories for illustrated specimens are: Natural History Museum, London (NHMUK); Centro de Investigaciones Paleobiológicas, Universidad Nacional de Córdoba, Córdoba, Argentina (CEGH-UNC); Lyon University 1, Lyon, France (FSL); Národní Muzeum (Barrande Collection), Czech Republic (NM-Bar.); National Museum of Wales (NMW).

Class Crinoidea Miller, 1821

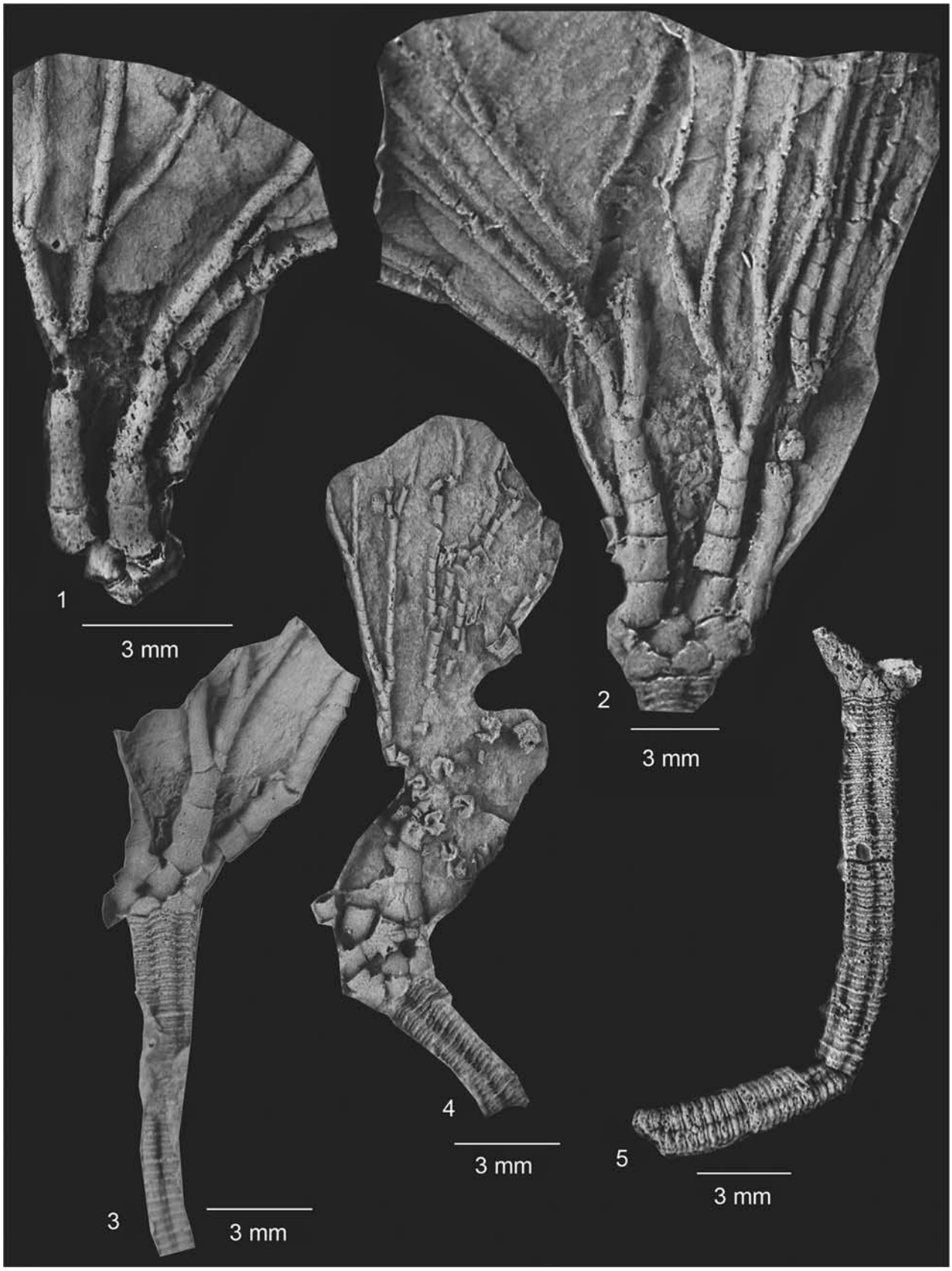

Figure 1. *Quechuacrinus ticsa* n. gen. and sp., latex casts, all flattened by compaction; (**1, 2**) holotype CEGH-UNC 23541, partly flattened, stem fractures to resemble pentameres, *1*, D ray view, cup folded under; (**2**) B ray view, C ray on left with projecting articulation from IBr_1 to longitudinal anal series, anal series folded under, depressed platelet field between and below arms; (**3**) paratype CEGH-UNC 23539, small interbasal gap; (**4**) paratype CEGH-UNC 23543, C ray view, irregular supernumerary plates below C radial; (**5**) paratype CEGH-UNC 23546, latex, much of stem, pentameric distal portion.

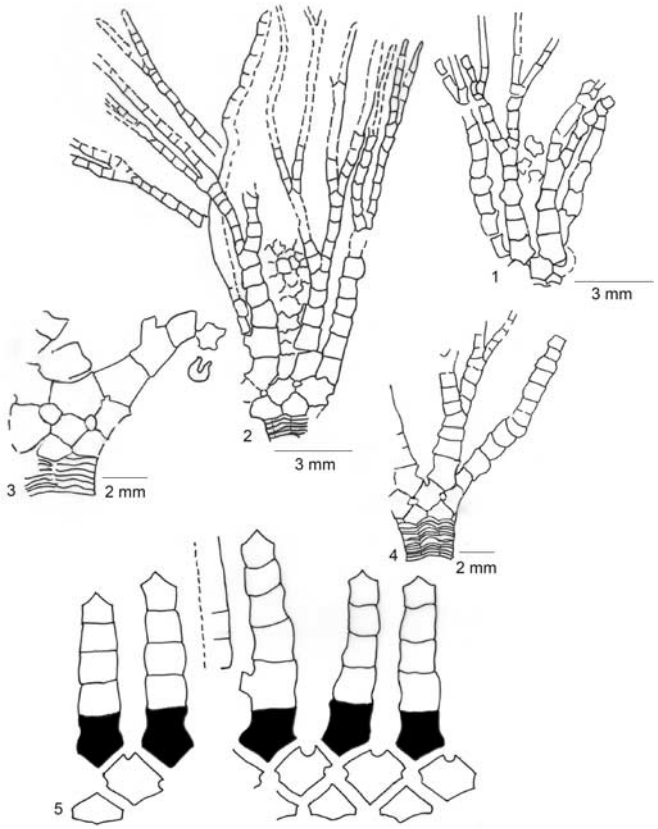

Figure 2. *Quechuacrinus ticsa* n. gen. and sp., line tracings of plating, expanded cup plate diagram; (**1, 2**) holotype CEGH-UNC 23541; 1, D ray view; (**2**) B ray view, projecting anal series ridge to left from C ray first primibrach, inset interbrachial plate field platelets, small interbasal gaps; (**3**) paratype CEGH-UNC 23543, irregular plating below C ray; (**4**) paratype CEGH-UNC 23539, interbasal gaps; (**5**) composite plate diagram, radials in black.

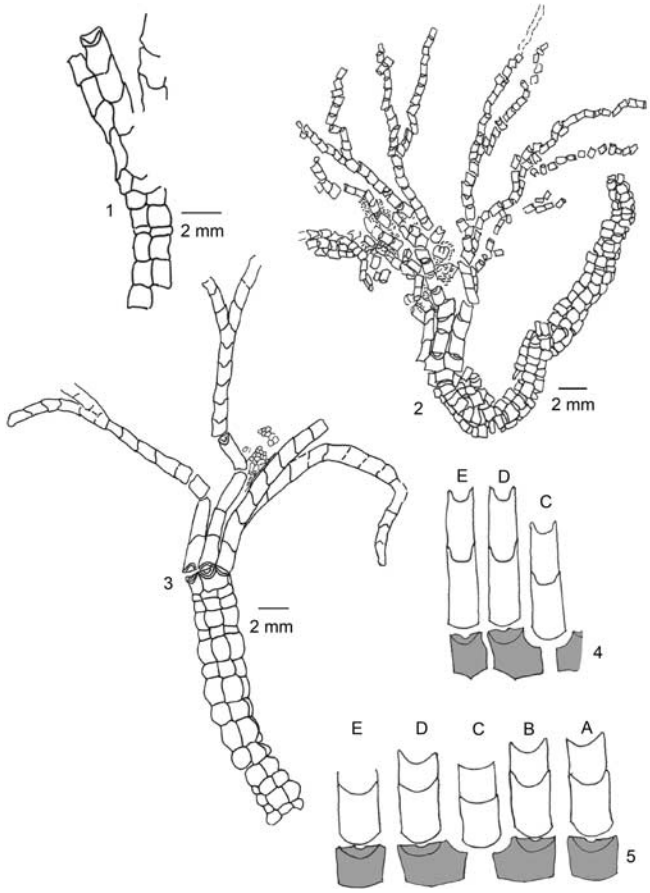

Figure 3. *Ramseyocrinus* species; line drawings; (**1, 3, 4**) *R. argentinus* n. sp.; (**1**) paratype CEGH-UNC 23548; (**3,4**) holotype, CEGH-UNC 23549, tracing and cup plate diagram with radials in grey, respectively; (**2, 5**) *R. vizcainoi*; (**1**) tracing; (**2**) cup plate diagram (modified from Ubaghs, 1983).

Subclass Camerata Wachsmuth and Springer, 1885
Order Unassigned
Family Reteocrinidae Wachsmuth and Springer, 1885

Diagnosis.—Camerates with truss-like ray ridges with intervening deep pockets or fenenstrae and a ray-like anal series, radials disjunct; arms and tegmen articulating at level of primibrachs or higher, tegmen covered by irregular platelets, irregular synostosial stem articulae.

Genus *Quechuacrinus*, new genus

Type species.—*Quechuacrinus ticsa* Guensberg and Waisfeld

Diagnosis.—As for the species, by monotypy.

Etymology.—*Quechua* is the pre-European language spoken by inhabitants of northwest Argentina; *crinum*, Latin, for lily.

Remarks.—*Quechuacrinus* resembles *Reteocrinus*, differing in posterior morphology and in having relatively smaller interbasal fenestrae (apical pits). *Cnemecrinus*, an earlier Floian reteocrinid (Guensburg and Sprinkle, 2003), expresses cup pockets exclusively rather than fenestrae and CD interray plating includes truss-like elements, smaller but similar to the anal series and primibrachs. By contrast, other reteocrinids, including *Quechuacrinus*, display depressed interbrachial platelet fields. Irregularly plated specimens of *Reteocrinus* have been described (Guensburg, 1984, pl. 4, fig. 13) and at least one example (Fig. 4.4) is known in *Quechuacrinus*.

Quechuacrinus ticsa, new species
Figure 1.1–1.5

Types.—Six specimens; the holotype CEGH-UNC 23541, and paratypes CEGH-UNC 23539, CEGH-UNC 23540, CEGH -UNC 23543, CEGH-UNC 23546, and CEGH-UNC 23547.

Diagnosis.—Reteocrinidae with small interbasal fenestrae, anal series joined to C ray.

Occurrence.—Acoite Formation, early Late Floian, northwestern Argentina.

Description.—A small reteocrinid, holotype crown height 17.7 mm without arm tips, paratypes slightly larger, holotype partly flattened cup 2.7 mm tall to radial tops and 4.1 mm wide at D, small interbasal gaps and smaller interbasal depressions;

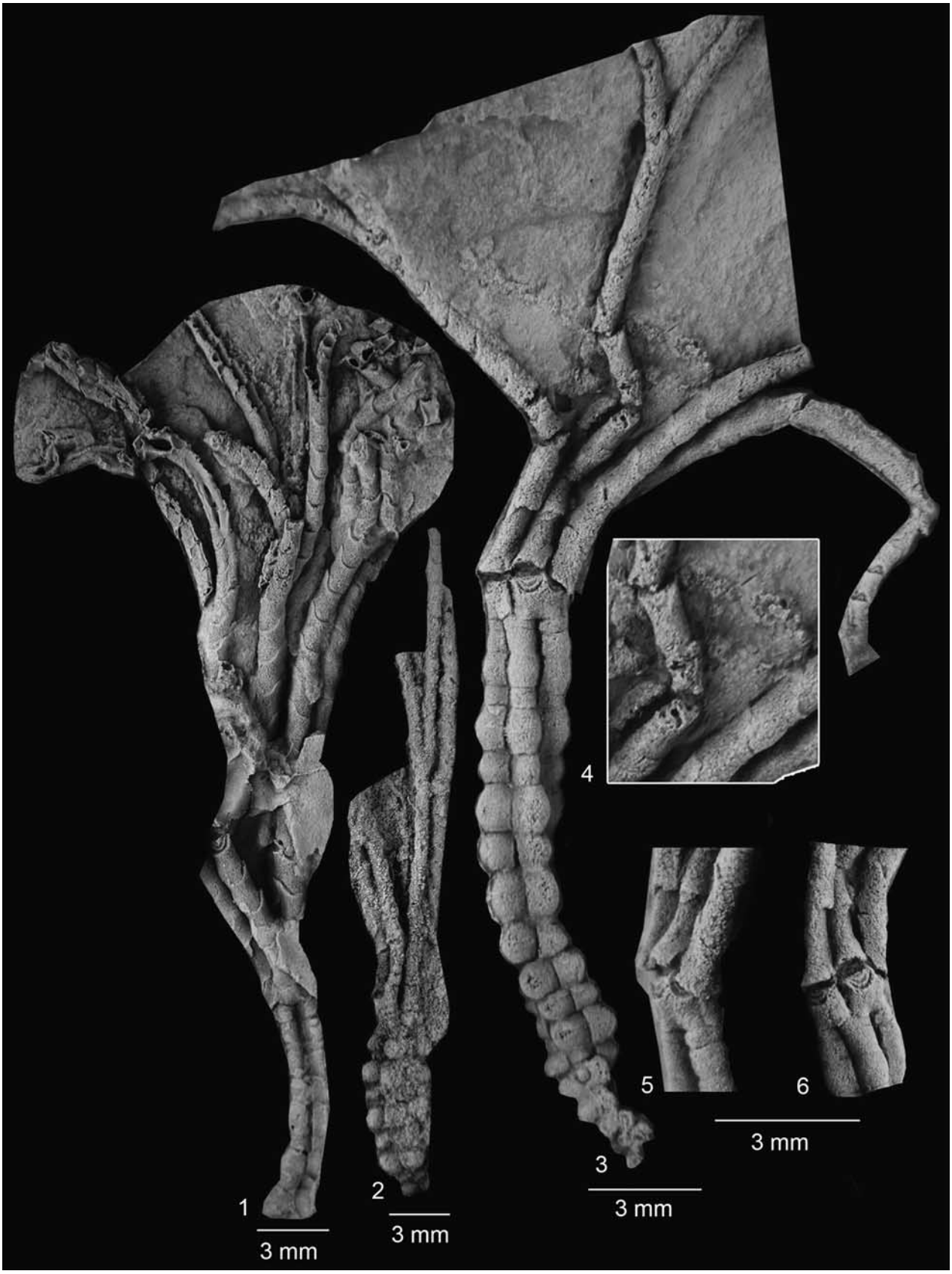

Figure 4. *Ramseyocrinus argentinus* n. sp.; (**1**) paratype CEGH-UNC 23548, anal sac platelets left center, at level of secundibrachs; (**2**) paratype CEGH-UNC 24633, coarse preservation; (**3–6**) holotype CEGH-UNC 23549, D view of crown and stem segment, anal sac detail, C view (C on right) of cup, and D view of cup, respectively.

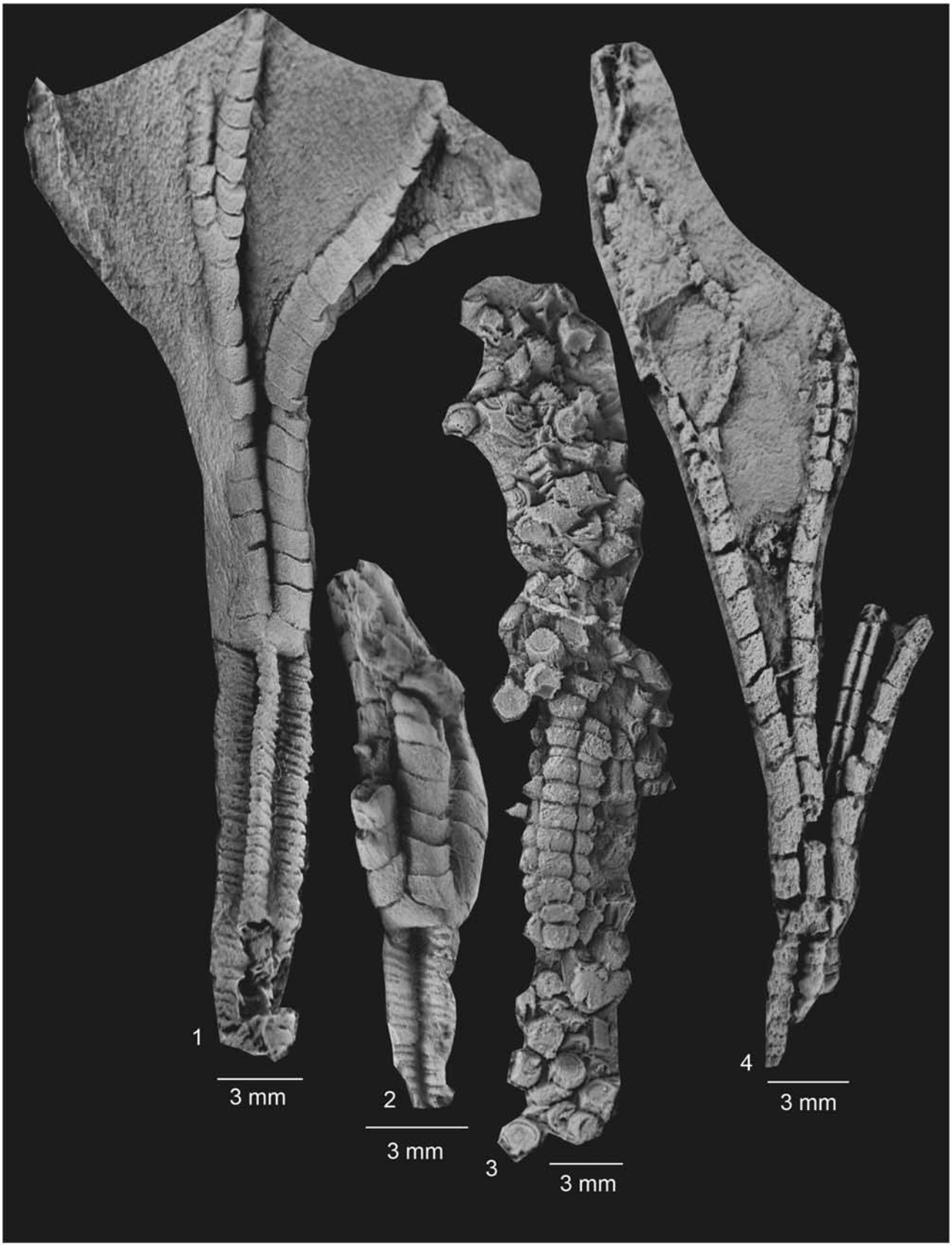

Figure 5. (**1, 2, 4**) *Ramseyocrinus cambriensis* (Hicks, 1873); (**1, 2**) latex casts of holotype NMW 29.308.G318 in A and CD views, respectivley; (**4**) NMW 86.93G.1a, referred specimen by Cope, 1988, CD view, coarse preservation; (**3**) *Ramseyocrinus vizcainoi* Ubaghs, 1983, FSL 712 076, referred specimen, proximal stem with disarticulated crown.

Figure 6. *Ramseyocrinus cambriensis* (Hicks, 1873); latex cast of referred specimen NHMUK E3, large crown and much of stem; (**1**) entire specimen; (**2**) distal stem segment; (**3**) crown and proximal stem; (**4**) mid-section of arms and well-preserved portions of granular anal sac.

Figure 7. *Entrochus primus*, NM-Bar. 35050 L13 304, oblique view of stem segment with monomeres, circular cross section, disjunct tetrameral lumen, and narrow crenularium.

primary cup plating stout; infrabasals small, with short mutual (lateral) contacts, lower surface with apex marking alternating stem mere boundaries, holotype A ray infrabasal 1.0 mm tall and 1.1 mm wide, C element slightly larger; basals squat Y-shaped, bounding interbasal gaps and interbrachials plate fields, BC element in holotype 1.2 mm tall and 1.1 mm wide; radials as large or larger than basals, squat inverted Y-shape, medially constricted, holotype C radial 1.2 mm tall and wide; primibrach series tapering, four in holotype B ray, five in C-ray; C first primibrach with small ridge articulating to anal series; arms long, thin, tapering, branching isotomously at least three times; brachials orthogonal; interbrachial plate fields depressed, of irregular but uniform platelet pavement merging with tegmen, upper extent of tegmen unknown; proximal to medial stem with slight distal taper accentuated by flattening; pentalobate cross section proximally, becoming rounded distally,? monomeric proximally, pentameric distally, irregular synostosial articulations; lumen and articular surfaces unavailable.

Etymology.—*Ticsa*, a nearby village to the type locality.

Remarks.—Abnormal specimens of *Reteocrinus* with irregular cup plating have been illustrated (Guensburg, 1984, pl. 4, fig. 13) and one example (Figure 4.4) is known in this taxon.

Subclass DISPARIDA Moore and Laudon, 1943

Diagnosis.—Crinoids with anal sac projecting from C-ray.

Remarks.—Guensburg (2010) diagnosed disparids as "crinoids expressing posterior plating augmented with an arm-like branch extending from the C-ray." The new diagnosis admits *Ramseyocrinus* and *Tetragonocrinus* where there is close association with the C-ray, but there is no arm-like branch.

Order Unassigned
Family Tetragonocrinidae Stukalina, 1980

Diagnosis.—Disparids with cup formed of four radial plates, anal plates lacking; at least one radial facet is compound formed by adjacent radials; anal sac arising from the tegmen and possibly the oral side of the C-ray. Stem tetrameric. (Emended from Stukalina, 1980.)

Genus *Ramseyocrinus* Bates, 1968

Diagnosis.—Tetragonocrinids with radials arranged in a bilateral pattern with two anterior small radials aligned with and underlying A- and E-rays, and two posterior large radials each aligned with and supporting B- and D-rays and a compound facet supporting the C-ray.

Ramseyocrinus argentinus new species
Figure 4.1–4.6

Types.—The holotype is a crown and proximal stem (CEGH-UNC 23549), paratypes include an incomplete crown (CEGH-UNC 23548), and poorly preserved crown (CEGH-UNC 24633).

Diagnosis.—*Ramseyocrinus* with relatively elongate plating, E radial higher than wide; anal sac of thin polygonal platelets.

Occurrence.—Acoite Formation, early Late Floian, northwestern Argentina.

Description.—Crown 18.4 mm tall in holotype lacking arm tips, partial paratypes approximately 50% larger; cup small, formed of four radial plates, here interpreted as A, B, D, and E elements, bilaterally symmetrical with A and B radials slightly taller than wide; B and D elements wider than tall each supporting their respective arms with full facets as well as half of C arm in a compound facet, C arm then is equally co-supported by half facets. Radial facets concave declivate, oriented approximately 45 degrees from horizontal, each with a pair of concentric arcuate grooves.

Tegmen not exposed; articulated lower portion of anal sac curved alongside C arm to level of fifth primibrach in holotype, reaching level of third secundibrach in paratype CEGH-UNC 23548, sac composed of platelet pavement, platelets irregular to partly elongate hexagonal, parallel to sac axis.

Arms long, stout, istomously branching at D and E arms primibrach 9 or 10 in holotype; distalmost branching unknown. Primibrach 1 taller than wide, primibrach height to width ratio decreases upward but taller than wide to at least secundibrachs; brachial facets s-shaped, surfaces with arcuate concentric grooves similar to those of radial facets.

Stem of strong lobate tetrameres; alternating with and forming triple junctures with radials; subsequent tetramere sets in alternating short and tall pattern; weakly tumid proximally grading to strongly tumid distally. Paratype CEGH-UNC 24633 expresses pronounced tumid stem meres.

Etymology.—*Argentinus* refers to the country of origin.

Remarks.—*Ramseyocrinus* species differ in plate proportions but share similar plate arrangement. The new species expresses taller stem, cup, and arm plating relative to the other two known species. *Ramseyocrinus argentinus* (Figs. 3.1, 3.3, 3.4, 4.1–4.6) is closest to *R. vizcainoi* (Figs. 2.2, 4.3) from the Floian of the Montagne Noire region of France but the latter's crown and stem plates are shorter. Specimens assigned to *R. cambriensis* exhibit great variation in overall size and plate proportions. Smaller specimens (compare Figs. 5.1, 5.2, 5.4, 6.1–6.3) more closely resemble *R. argentinus*. A well-preserved large specimen shows parts of a large anal sac formed of granular plating and shorter tetrameres.

Entrochus primus (Waagen and Jahn, 1899) (Fig. 7) from the early Middle Ordovician of the Czech Republic has been assigned to *Ramseyocrinus* (Donovan, 1984). Type material consists of stem fragments alone. These are monomeric, circular in outline, with narrow but well-defined crenularium, and a disjunct tetrameric lumen. These expressions contrast from other fossils assigned to *Ramseyocrinus*. We exclude this taxon from *Ramseyocrinus*.

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