Revised extraxial-axial homologies in Asteroidea

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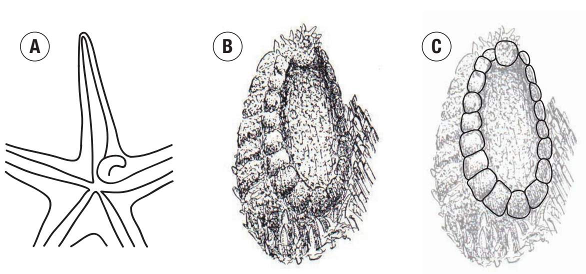
Multiple lines of evidence are used to identify the growth zones that produce asteroid arms. Evidence includes skeletal morphology, growth series specimens, regenerating specimens, branch-arm and arm stump specimens, positional information theory, regeneration models (distal-signaling), and identifying rudiment-derived and non-rudiment-derived body wall in the post-larvae.

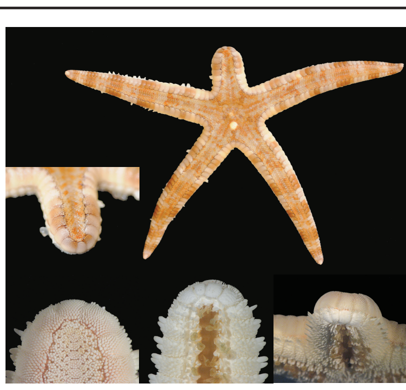


Astropecten aurantiacus (R=146mm, r=32mm) with a 15mm undersurface supernumerary branch-arm, described by Zirpolo (1928). A. Branch arm location. B, C. Oblique view of branch arm; terminal plate at top; terminal plate and superomarginals (SMM) highlighted in C. All figures after Zirpolo (1928).

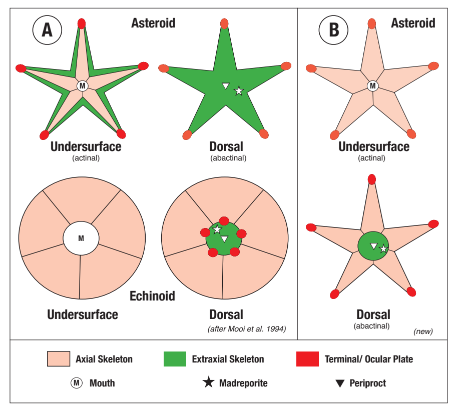
The SMM of the two sides have joined and enclose a quasi-elliptical area behind the terminal plate. Paxillar abactinal arm skeleton is confined within this enclosed area. This establishes that the paxillar plates of the abactinal arm skeleton are products of the growth zone at the arm tip: they are partly axial skeleton (ocular plate rule [OPR]), and partly gusset plates that are developmentally secondary to the OPR-formed SMM.

The free part of the undersurface branch-arm is anatomically complete, with species-typical actinal, abactinal, and ambital surfaces. The undersurface branch-arm has no contact with the abactinal or ambital body wall of the ‘parent’ animal, but nevertheless the undersurface arm has anatomically correct abactinal and ambital body wall and skeleton. It is deduced from this that the growth zone generates anatomically complete arms: the growth zone fully surrounds the terminal plate.

The OPR tells us that the arms produced by this growth zone are comprised only of axial body wall and the skeleton produced by this growth zone is comprised only of axial skeleton.

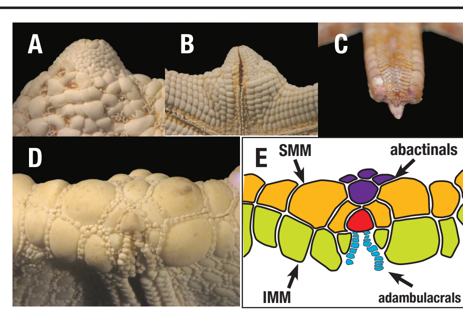


Archaster angulatus (USNM 1139740) with arm stump that healed and did not regenerate the arm. The plates arc smoothly and join on the midline. This distinctive non-regenerating stump condition indicates that positional information in the asteroid arm is left-right symmetrical, and that outgrowth of the asteroid arm is by intercalation between a full-surround distal-signaling center and the last-formed section of arm (Hotchkiss 2009, Hotchkiss & Keesing 2012, Hotchkiss 2012). Photographed alive by J. Keesing (top images); bottom images dry.



Diagrams of asteroid and echinoid growth zones and extraxial-axial theory (EAT) body wall homologies. A. According to Mooi et al. (1994) and Mooi & David (1997, 2000). B. As proposed herein.

The revision is that the asteroid arm lacks extraxial skeleton. In A, axial skeleton is produced only at the edge of the terminal/ocular plates that is directed toward the mouth (adoral edge). In B, the asteroid growth zone produces axial skeleton in the full surround of the terminal plates. In B, asteroid arms are composed only of axial skeleton and of gusset plates that are developmentally secondary to the axial skeleton (actinal, intermarginal, and dorso-lateral gusset plates not separately diagrammed).

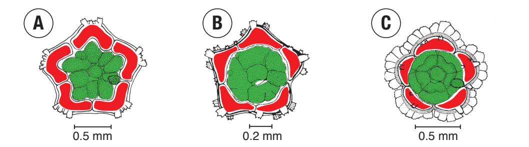


Regenerating arm tips help to determine growth zones because the blastema of regeneration is also the blastema of normal growth. Growth zones encompass all the plates ontogenetically related to a given terminal plate, plus the terminal plate itself. The youngest plates are next to the terminal plate.

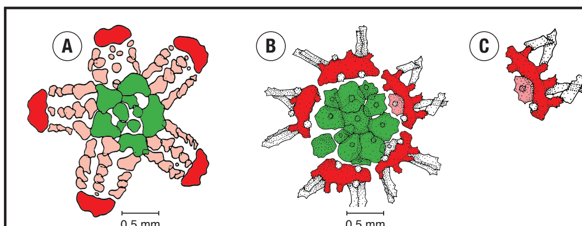
A, B. Abactinal and undersurface views of *Linckia laevigata* (USNM 1111695) with a regenerating arm; the smallest regenerating ambulacral, adambulacral, inferomarginal (IM), superomarginal (SM), and abactinal plates are in contact with the terminal; the regenerating arm is already integrated into the body contours.

C. Oblique abactinal view of regenerating arm tip of live *Archaster angulatus* for comparison with arm stump specimen (photo by J. Keesing).

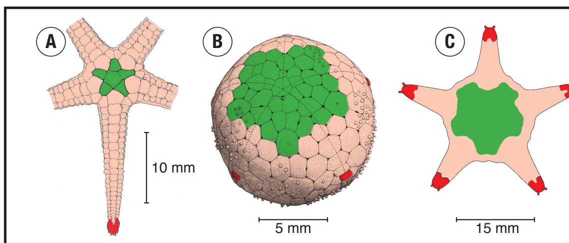
D, E. Edge view of *Pentagonaster pulchellus* (MPRI 0289) with one regenerating arm; the smallest regenerating adambulacral, IM, and SM plates are in contact with the terminal (red); ambulacral plates within the furrow not visible; the midradial abactinal plate is judged not a regenerated plate based on large size and because it is occluded from touching the terminal plate.



Terminal plates in earliest growth stages form an uninterrupted boundary that separates abactinal disc extraxial skeleton (shaded green in the drawings) from rudiment-derived oral surface plate systems. Abactinal views of: A. *Linckia laevigata*; B. *Culcita novaeguineae*; C. the 5-armed imago of *Acanthaster planci*. (all after Yamaguchi 1973).



Growth stages in which the boundary between the abactinal disc plating (green) and the beginnings of the arm skeleton can be seen. Demonstration of the boundary in these growth stages predicts that the boundary is present also in later growth stages. A. *Leptasterias ochotensis similispinus* (after Kano et al. 1974). B, C. *Astropecten latespinosus* (after Komatsu 1975). C. Terminal plate with OPR-formed midradial abactinal.



The boundary between extraxial abactinal disc plating (green) and arm skeleton is neatly demonstrated in (A) *Cnemidaster wyvillii*, and plausibly inferred in (B) *Podosphaeraster polyplax* and (C) *Porcellanaster caeruleus*. (A, C, after Sladen 1889; B, after Clark & Wright 1962).

As analyzed here, the growth zones develop arm plates in the full surround of the arm tip. This is congruent with regeneration models. The OPR applies individually to asteroid ambulacrals, adambulacrals, IMM, and SMM. Midradial abactinal plates form either consistent with the OPR, or as gusset plates that are developmentally secondary to superomarginals. Plate series that obey the OPR are defined to be axial skeleton. Secondary development of gusset plates does not change the status of OPR-formed axial plates. Gusset plate systems are often well supplied with papular pores.

An application is to understand the evo-devo origin of arms as outgrowths: the event that led to outgrowth of asteroid arms was acquisition of distal-signaling around the full periphery of each arm tip (full-surround distal-signaling).

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