1 Introduction

One of the most fundamental factors affecting our ability to understand the evolutionary history of Echinodermata, a long-lived, diverse, and complex phylum of marine organisms, is our ability to identify homologous skeletal elements and regions across different clades. Homology forms the basic underlying assumption set at the root of the morphological data used to infer phylogenetic relationships, allows for understanding the evolution of function, and many other lines of research within the clade. Unfortunately, the homology of skeletal elements is often masked through evolutionary processes that result in character transformations that alter the presentation of characters so that they are unrecognizable, are confused for other morphologically similar character states, or lose their features altogether (Sumrall, 2017). Without an accurate understanding of homology, it is not possible to correctly infer phylogenetic relationships. Identifying homologous elements requires examining morphological features across taxa and through a number of lenses. Extant echinoderms (asteroids, ophiuroids, holothuroids, echinoids, and crinoids) evolved early in the group's history and offer insights from larval morphologies, development, and gene expression, but are strikingly different from the extinct clades of Paleozoic echinoderms, such as blastozoans and homalozoans that have no modern representatives. Paleozoic forms have greater taxonomic and morphologic diversity, but the high levels of convergence, and disparate bauplans throughout their evolutionary history (Ubaghs, 1971; Sumrall, 2017; Deline et al., 2020) have complicated our ability to unravel the origins, ontogeny, evolution, and life mode of these animals.

Echinoderms have a biomineralized skeleton of mesodermal origin (see Gorzelak, 2021). The development of the biomineralized echinoderm skeleton is associated with a distinct set of transcription factors, signaling molecules, and differentiation genes, which all act together during development and comprise the biomineralization toolkit of echinoderms (see review in Thompson 2022). It is the expression of the components of this biomineralization toolkit in particular cells, typically referred to as skeletal cells, which underlies skeletal growth and development, and many skeletal cells occupy the porous cavities that characterize echinoderm stereom (Czarkwiani et al., 2016; Thompson, 2021). The location and molecular fingerprint of these skeletal cells is controlled by distinct spatial signaling cues which are sent from the ectoderm (Duloquin et al., 2007, Czarkwiani et al., 2021). It may be that the activity of these signaling molecules in distinct tissues may result in the presence or absence of skeleton in particular portions of the body wall (Zamora et al., 2022). However, while it has been demonstrated that different components of the echinoderm

biomineralization toolkit are expressed in different biomineralized structures (Piovani et al., 2021), there is so far no evidence to indicate that the expression of distinct biomineralization genes is associated with particular skeletal plates that could form the basis for a homology scheme.

Patterson (1982) proposed three tests to falsify hypotheses of homology: two a priori tests (similarity and conjunction) and one a posteriori test (congruence). The test of similarity proposes that hypotheses of homology between two structures could be supported if they are similar in construction. The test of conjunction proposes that hypotheses of homology between two structures assumed to be a singular character transformation are falsified if those two structures are both present in the same organism. The a posteriori test of congruence states that if a character transformation appears more than once optimized on a phylogenetic tree, the feature must have evolved more than once and is therefore rejected as homologous. For a full discussion of echinoderm homology examples of each of these tests, refer to Sumrall (1997).

Difficulties in identifying homologous elements are further compounded by human efforts to define evolutionary relationships. Long-standing methods of delineating taxonomic groups, dating back to the first attempts at classification (Linnaeus, 1758), emphasized differences among taxa rather than emphasizing similarities that can be used as evidence to recognize taxa. Further, taxonomists have defined distinct and often conflicting sets of terminology for individual groups, making it difficult to discuss homologous elements that groups might share (Sumrall, 2017). This concept is prominent in Paleozoic echinoderm clades, where many classes have different and incompatible lexicons of morphological terms describing homologous morphology. Horizontal comparisons of terms show these include multiple names for homologous morphologies and the same term being used for a variety of nonhomologous morphologies (Sumrall, 2010; Sumrall and Waters, 2012; Sheffield and Sumrall, 2019; Ausich et al., 2020).

Additionally, there are issues with definition and diagnosis, similar to Rowe's (1988) discussion of these terms with respect to a clade, when applying many homologous terms to blastozoans. Rowe (1988) used definition to describe a clade as a historical entity based on ancestry, for example, a most recent common ancestor and all descendants. This is distinct from a diagnosis, which is used to identify group membership based on attributes. In practical terms, for example, glyptocystitoid rhombiferans are often diagnosed by a series of features such as the plating of the theca, the presence of dichoporite respiratory structures, and morphologies of the stem (Zamora et al., 2017). Because such diagnostic structures are not universally found among all taxa, including stem lineages arising prior to their evolution and character losses in derived taxa,

a simple diagnosis is not sufficient to circumscribe all relevant taxa. This creates diagnoses such as "feature present unless secondarily lost," which requires a priori knowledge of the phylogenetic placement of a taxon to diagnose it as a member of the clade. However, by defining taxa based on shared ancestry within the context of an evolutionary tree, we can circumscribe them as a clade and the presence of diagnostic traits becomes irrelevant to our understanding of their group membership (Brochu and Sumrall, 2001). Optimized onto the phylogeny, diagnostic traits can be seen to evolve within a series of nested clades and these traits are evidence used to understand the structure of the tree. But, modern phylogenetic methods define taxa based on tree structures, rather than as objects that bear suites of characters.

In many respects, homology can be seen in a similar framework. Because homologous structures can be defined by their evolutionary origin as a synapomorphy and have a fate as character state transformations in descendant lineages, clades are recognizable by bearing diagnosable alternate states in the character description. Homology is defined based on the historical origin of structures – if structures are derived from a common ancestral origination, such as a bird wing and a whale flipper are, then at the level of forelimbs they are homologous. In practice, however, we often rely on diagnosis, where we assume homology because two structures have a common construct that can be identified. We can list the features that we expect a given structure to have and, if they are present, then we assume the homology, but true homology can only be understood within a historical framework.

Given the lack of developmental information in many cases, inferring homology based on a diagnosis is indeed problematic, but often unavoidable. Homology is clearest where there is ontogenetic information, and tracing specific skeletal elements throughout ontogenetic stages provides strong evidence for their homology and their identification in mature specimens. The plates that cover the mouth in most echinoderms, the primary peristomial cover plates (PPCP), are present in all identifiable early postlarval taxa, where known, including edrioasteroids, crinoids, blastoids, and a host of other stemmed echinoderms (Sumrall and Waters, 2012). These plates can be traced ontogenetically and are often quite evident in mature specimens of these taxa. This information can then be applied to other taxa that descend from a common ancestor. In other cases, such as plating of the axial skeleton, the developmental pathway can be seen in the presence of terminal growth of the axial plate series. Of course, there are clear limitations concerning ontogenetic data in the fossil record, as many groups of fossils are not represented by different growth stages (e.g., many diploporans have few documented juvenile forms; Sheffield et al., 2018).

In EAT (see below), the imperforate and the perforate extraxial skeleton are treated as separate entities, defined in recent taxa by their origination, growth, and development, but in fossils they are diagnosed by their character expression, which is subject to heterochrony and heterotopy. Consequently, inferring homology based on a diagnosis is not universally reliable. Numerous other examples in Paleozoic echinoderms indicate that the distinctions between perforate and imperforate extraxial skeleton may have little to do with the underlying developmental pathways but are diagnosed instead by the expression of ephemeral morphological features (Fig. 1). In what follows, we analyze homology hypotheses for major features of echinoderm bodies: (1) respiratory structures; (2) feeding structures; (3) hydropores, gonopores, and periprocts; and (4) oral surface plating. As UEH (see below) was developed for plates of the oral area and ambulacral system, we cannot provide an analysis of each of these major features through both UEH and EAT.

This Element, focusing on homology hypotheses, requires a grasp of echinoderm morphologies. It is outside the scope of this review to introduce the details of morphology and body plans for the major echinoderm groups we discuss herein. Here, we provide references focusing on morphological features and body plans for these major groups. As echinoderm morphology is highly disparate, we refer readers to a large body of literature: Blastozoa (Sprinkle, 1973; Sumrall and Waters, 2012; Sheffield et al., 2022); Crinozoa (Kammer et al., 2013; Ausich et al., 2020); Echinozoa (Smith, 1984a; Kerr and Kim, 2001); and basal echinoderms (Parsley, 1980; David et al., 2000; Smith 2005; Zamora et al., 2012; Zamora and Rahman, 2014).

There are two foundational hypotheses for understanding echinoderm homology: (1) extraxial–axial theory (EAT; Mooi et al., 1994; Mooi and David, 1997; David and Mooi, 1998) and (2) universal elemental homology (UEH; Sumrall, 2010; Sumrall and Waters, 2012). The EAT hypothesis is built upon parameters of growth and development in extant echinoids and provides homology designations for different skeletal regions of the echinoderm body plan. This coarsely divides the echinoderm body plan into two regions differentiated upon their mode of growth: the axial region (essentially, the ambulacral system and related structures) and the extraxial skeleton (Fig. 2). The extraxial skeleton is further subdivided into the perforate and the imperforate extraxial skeleton based upon the presence or absence of piercings of the body wall. From the fossil perspective, the UEH hypothesis is built to recognize homology of individual skeletal elements of the peristomial border and axial skeleton across different groups of echinoderms. In essence, the UEH hypothesis refines homology

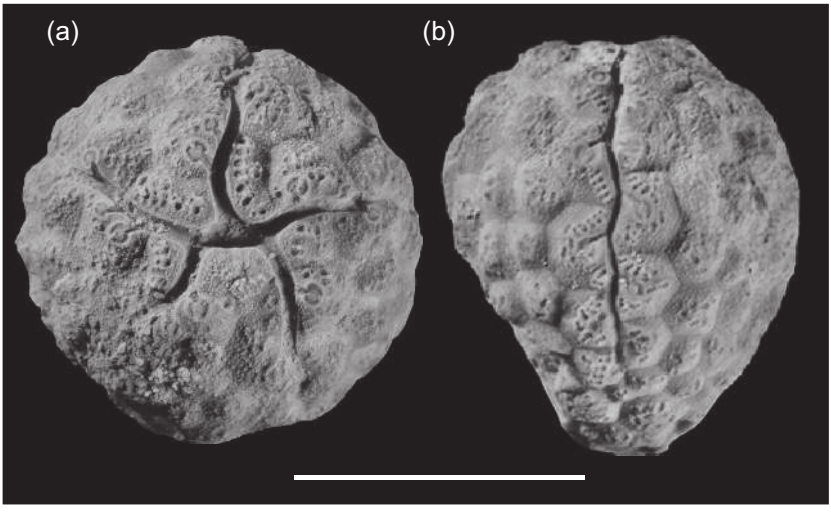

Figure 1 Respiratory structures piercing axial skeleton. (a) Oral view of *Estonocystis antropoffi* (GIT 540–80). The five ambulacral grooves lie on oral plate sutures; brachiole facets begin after the oral plate series and continue down the theca. (b) Side view of *Estonocystis antropoffi* (GIT 540–80). The ambulacra anastomose down the theca; short food grooves that connect with the main food groove lead to brachiole facets. These brachiole facets are contained within the center of single ambulacral floor plates, and diplopores align horizontally along the floor plates. In EAT, diplopores should be contained within perforate extraxial plates of the theca, while floor plates belong in the axial system. Both are modified from Sheffield and Sumrall (2019). Specimen whitened with ammonium chloride sublimated. Scale bar = 10 mm.

of the axial skeleton so that commonalities among plates of the oral region and ambulacra can be understood across pentaradial echinoderms. This system is limited by the lack of recognizable homologous features in the oral area of fossil eleutherozoans and homalozoans and scant knowledge of the earliest stages of development from extinct taxa. Extraxial–axial theory and UEH are often discussed as frameworks that exist in opposition to one another; we clarify here that they are compatible and capable of complementing one another to better our understanding of echinoderm homology (Sumrall and Waters, 2012). Herein, we provide a thorough review of both EAT and UEH and offer new insight on combining the two approaches. We also review future research directions utilizing these homology hypotheses with echinoderm taxa bearing unusual morphologies.