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**REVIEW**

# Deconstructing the long-standing a priori assumption that serial homology generally involves ancestral similarity followed by anatomical divergence

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**Abstract**

It has long been assumed that serial homologues are ancestrally similar—polysomerism resulting from a “duplication” or “repetition” of forms—and then often diverge—anisomerism, for example, as they become adapted to perform different tasks as is the case with the forelimb and hind limbs of humans. However, such an assumption, with crucial implications for comparative, evolutionary, and developmental biology, and for evolutionary developmental biology, has in general not really been tested by a broad analysis of the available empirical data. Perhaps not surprisingly, more recent anatomical comparisons, as well as molecular knowledge of how, for example, serial appendicular structures are patterned along with different anteroposterior regions of the body axis of bilateral animals, and how “homologous” patterning domains do not necessarily mark “homologous” morphological domains, are putting in question this paradigm. In fact, apart from showing that many so-called “serial homologues” might not be similar at all, recent works have shown that in at least some cases some “serial” structures are indeed more similar to each other in derived taxa than in phylogenetically more ancestral ones, as pointed out by authors such as Owen. In this article, we are taking a step back to question whether such assumptions are actually correct at all, in the first place. In particular, we review other cases of so-called “serial homologues” such as insect wings, arthropod walking appendages, Dipteran thoracic bristles, and the vertebrae, ribs, teeth, myomeres, feathers, and hairs of chordate animals. We show that: (a) there are almost never cases of true ancestral similarity; (b) in evolution, such structures—for example, vertebra—and/or their subparts—for example, “transverse processes”—many times display trends toward less similarity while in many others display trends toward more similarity, that is, one cannot say that there is a clear, overall trend to anisomerism.

**KEYWORDS**

anatomy, anisomerism, convergence, evolution, heteronomy, homologues, homonomy, polysomerism, serial homology, similarity

**1 | INTRODUCTION**

It has long been assumed that ‘serial structures’ are ancestrally similar—polysomerism, reflecting an ancestral metamerism resulting from a

“duplication” or “repetition” of homonomous forms—and then often diverge, for example, as they become adapted to perform different tasks such as the case in the forelimb versus hind limb of humans—anisomerism (e.g., Diogo, Linde-Medina, Abdala, & Ashley-Ross, 2013;

Diogo, Ziermann, & Linde-Medina, 2015; Gegenbaur, 1859; Gregory, 1934; Grimaldi & Engel, 2005; Koussoulakou, Margaritis, & Koussoulakos, 2009; Wagner, 2001). The work that covers in more detail the history of the idea of serial homology, which is, unfortunately, mostly neglected by scientists working on this subject, probably because it was written in French, is Schmitt's, 2004 book "Histoire d'une question anatomique: la repetition des parties".

As noted by Schmitt (2004), one fascinating aspect about serial structures is that the assumption that they are ancestrally similar, which is of crucial importance within the fields of comparative anatomy, functional morphology, evolutionary biology, developmental biology, and evolutionary developmental biology (Evo-Devo), has not been analyzed in detail in face of available empirical data. In reality, the earlier authors that studied in some detail cases of "serial homology", such as Owen, actually stated that the similarity between the "repeated" parts within an organism is often higher in "derived" taxa than in "basal" ones. It is important to stress that serial or "iterative" homology (homology of parts within a single body) originally referred to segments and bilateral counterparts in a comparative, not in an evolutionary, context. Historically, the idea that, for example, the structures of the forelimb and hind limb of tetrapods are "serial homologues" was first proposed by Vicq-d'Azyr (1774), and only much later by Oken (1843), and Owen (1849, p. 184), the two latter authors being deeply influenced by Goethe and the German romantics, and their obsession by polysomeric "ideal" archetypes (e.g., Diogo et al., 2013; Richards, 2004; Schmitt, 2004). That is why Owen actually referred to three types of homology: "special homology" refers to the concept of homology followed nowadays, for example, the forelimb of a human and the wing of a bird; "general homology" refers to that same homology, but applied to all taxa within a natural group of animals and their "archetype"; "serial homology" concerns "repeated" parts within a same organism (Owen, 1848). A major recurrent problem with the notion of serial homology, and in particular, the a priori assumption that serial homologues are originally similar, is precise that these definitions were not framed within an evolutionary context, but instead within an idealized theoretical "archetype" one. In fact, a major paradox, resulting from this historical context, is that what is nowadays called "serial homology"—for instance between the structures of the forelimb and lower limb, refers instead, in evolutionary terms, to what is now consensually called "evolutionary parallelism", which is therefore a subset of homoplasy, and not of true homology (Diogo et al., 2013). Indeed, the most striking examples of similarity between the forelimb and hind limb cited by Owen (1849) mainly refer to tetrapods with highly derived limbs (e.g., bats, horses, and plesiosaurs), and Owen specifically employed the term "parallelism" to refer to them, much more often than he used "serial homology". For example, when Owen discussed outgroup lineages to tetrapods, such as chondrichthyans, he clearly stated that those taxa "confuse" the notion of "archetype" and "serial homology" (Owen, 1849). That is, Owen clearly seems to be referring to homoplasy as has been later defined by evolutionary biologists, rather than the idea of serial homology followed by most evolutionists since then (Diogo et al., 2013). That is, although Owen's classification system was not based on evolutionary

transformation, he did refer to "higher" versus "lower" taxa, with the "higher" taxa, more derived from the idealized "basal archetype", often having more similarity between the forelimb and hind limb. This idea is similar to that explicitly defended later by Lankester (1870), who stated that the forelimb and hind limb became more similar with time: he considered the majority of cases of "serial homology" to be homoplastic, that is, cases of derived similarity likely due to the influence of forces or similar conditions or "correlations of growth" (Schmitt, 2004, 2017). A similar line of reasoning was postulated by Spemann (1915), who argued that to talk about "serial homology" it is more acceptable to refer to homoplasy, since the latter concept is more focused on a mechanistic rather than a phylogenetic explanation of embryonic development and its forces/correlations (Schmitt, 2017).

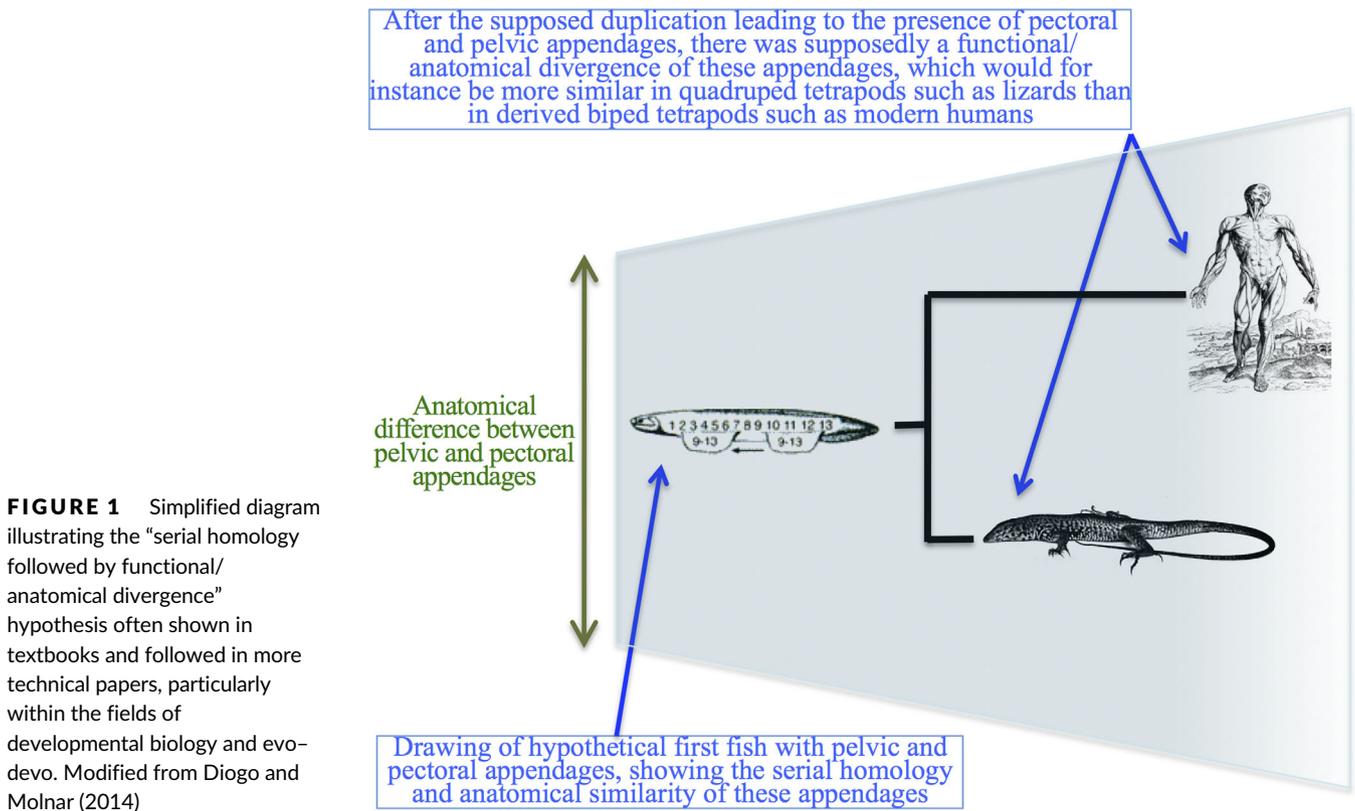
The current conceptual difference between developmental biologists and evolutionary biologists concerning the idea of serial homology is also related to these historical facts. That is, the former tend to emphasize similar developmental mechanisms ("developmental serial homology" *sensu* Wagner, 1989, 1994, 2001, 2007, 2014; see also Gilbert & Bolker, 2001; Ohde, Yaginuma, & Niimi, 2014; Schachat, Oliver, & Monteiro, 2015) while the latter tend to stress both anatomical similarity and evolutionary continuity ("historical serial homology" *sensu* Wagner, 1994; Brigandt, 2003; see Miyashita & Diogo, 2016). Recently, Reno, Horton, and Lovejoy (2013) applied the following criterion to refer to evolutionary/historical serial homology: "confirmation of its *evolutionary continuity* throughout a lineage, such that the structure can be shown to have a *shared ancestry* with segmental duplicates within the same body (paralogues, usually named serial-homologues) or similar structures in other lineages (orthologues, usually named homologues)". That is, in the overall, either as defined by developmental biologists and by evolutionary biologists nowadays, the idea of serial homology is indeed different from Goethe's romantic idea of polysomeric archetypes, which *did not refer to an ancestral serial pattern*, but rather to a *theoretical, ideal potential pattern* that could be achieved *via vitalist forces* (Richards, 2004). Moreover, it is also important to note that authors such as Bateson (1894) not only contradicted the paradigm of ancestral similarity of serial structures by stating that they are actually never completely similar ancestrally, but also stated that "serial homology" cannot truly have an historical/evolutionary definition, as does homology (Schmitt, 2004). Authors such as Boyden (1943) also contradicted the paradigm of ancestral similarity, noting that "serial" structures can never be truly ancestrally similar because even if they share similar genetic mechanisms, they are formed in different parts of the body (Schmitt, 2004, 2017). Boyden clearly stated that "serial homologues" (homotypes) actually commonly differ between themselves much more than "true homologues", for example, the difference between the mouth parts and the legs within one same crustacean individual is greater than the difference between the legs of different crustacean species (Schmitt, 2017). Unfortunately, these views are usually not taken into account by researchers working on serial homology, who tend to accept the a priori assumption of ancestral similarity followed by derived divergence, either because they do not go into the historical details or because this assumption was explicitly defended by Darwin (1859)

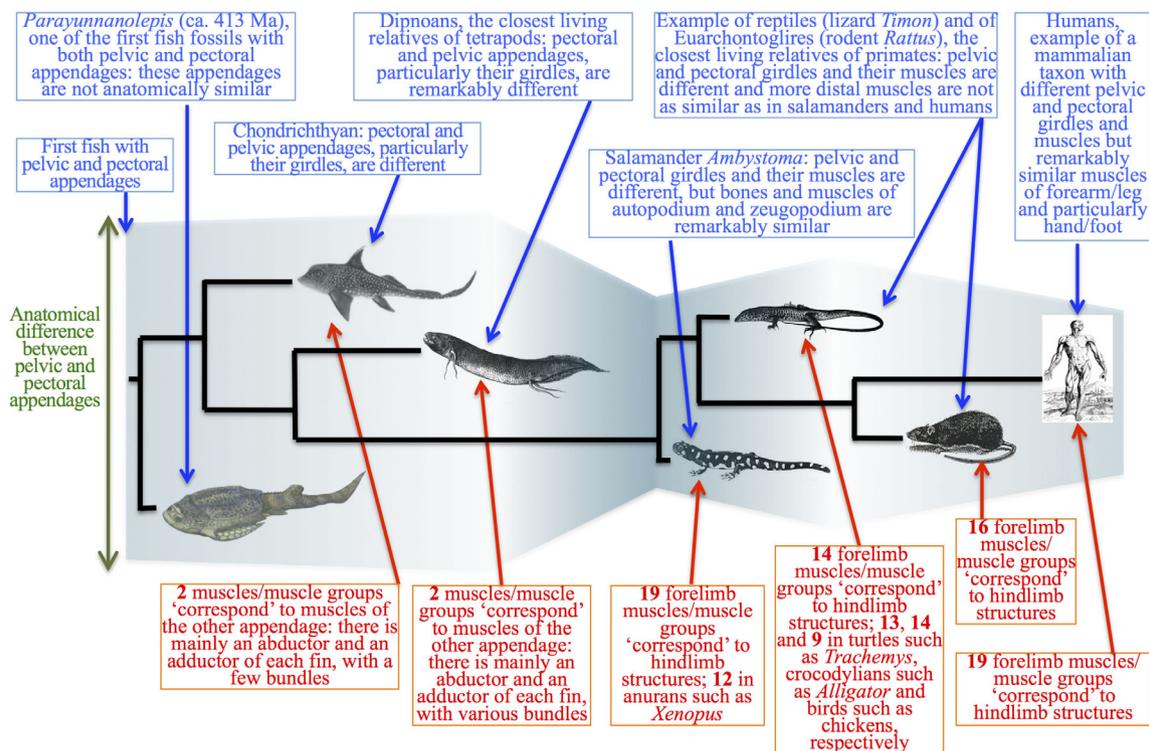
and then became almost a paradigm in evolutionary biology. Several recent examples of authors/works accepting a priori this paradigm are provided, for instance, in the extensive literature reviews of Schmitt (2004, 2017), Diogo et al. (2013), and Miyashita and Diogo (2016), and references therein.

However, contrary to this paradigm—and as would be expected by those that do know in detail the historical theoretical problems concerning the idea of serial homology—the more data that is available, the more this dogmatic a priori assumption of ancestral similarity followed by derived divergence is put in question. For example, recent works on vertebrate comparative anatomy, as well as molecular knowledge of how serial structures are patterned along the antero-posterior body axis of bilateral animals and how “homologous” patterning domains do not necessarily mark “homologous” morphological domains, are strongly contradicting this a priori assumption. As Boxshall (2013, p. 249) questioned in his recent review on arthropod limbs and their development, “the first cephalic limb of euarthropods has a single proximo-distal axis and thus differs from post-antennular limbs which are primitively biramous. [...] how fundamental is this distinction, given that well-known homeotic mutations, such as the Antennapedia mutant of *Drosophila*, indicate that antennules and post-antennular limbs can be viewed as serial homologues?”. As he noted, “indeed, numerous homeotic mutations are now known that can transform maxillary palps, labial palps and genitalia into antennae or thoracic legs in a variety of insects, not just *Drosophila*”. That is, structures that would be developmentally/molecularly considered to be serial homologues are often actually different from each other, morphologically. According to him, the major reason for this is that

the serial homologues are specified at different anterior–posterior regions of the body: “the shared common features between antenna and leg development in *Drosophila* indicate that, despite some significant differences, the antennules and post-antennular limbs of all arthropods can be viewed as serial homologues, but specification of the anterior-most limb as antennule ensures that it develops as a single axis rather than biramous limb” (Boxshall, 2013, p. 250). Importantly, in his conclusions, and based on his review, he stressed that “comparative data from different arthropod taxa show that homologous patterning domains do not necessarily mark homologous morphological domains...at present, it seems unlikely therefore that gene expression patterns will provide us with reference points allowing the identification of homologies between the component segments of chelicerate, insect, myriapod and crustacean walking limbs” (Boxshall, 2013: 262). That is, as summarized by him, “there remains a major gap in our knowledge—the gap between the new paradigm emerging from developmental genetics and the morphological study of phenotypes”.

It is important to note that the “ancestral similarity-derived divergence”—or “polymerism followed by anisomerism”—assumption (Figure 1) is not only put in question by such studies showing that at least some serial homologues are ancestrally different anatomically, but also by recent studies that have empirically shown that some of the most emblematic “serial-homologue” structures actually became *more* similar with time, exactly as noted by Owen. That is, they are truly cases of evolutionary parallelism, and thus of historical/evolutionary homoplasy, as stated by Lankester (1870). For instance, as seen in Figure 2, the overall anatomical similarity between the muscles





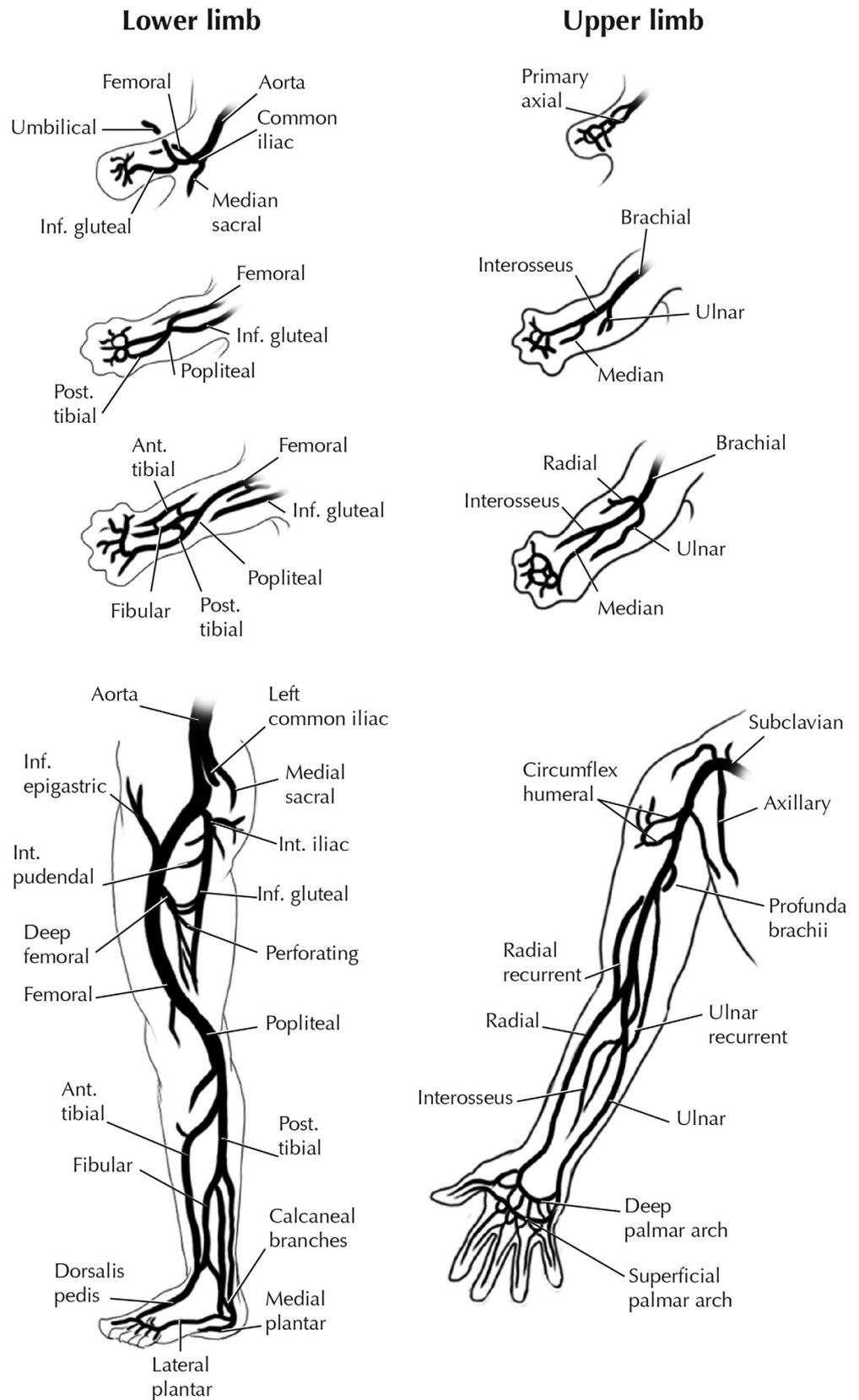
**FIGURE 2** Simplified diagram of the evolutionary transitions in muscle anatomy leading to modern humans. The evolutionary history of the pelvic and pectoral appendages is much more complex than the “serial homology followed by functional/anatomical divergence” hypothesis suggests. Complex interplay between ontogenetic, functional, topological, and phylogenetic constraints leads to cases of anatomical divergence followed by convergence (similarity bottlenecks). Modified from Diogo and Molnar (2014). PEL, PEC, pelvic and pectoral appendages

of the forelimb versus the hind limb is higher in primates such as humans than in taxa such as mice and lizards and then what the phylogenetic studies on the evolution of these muscles have reconstructed for the last common ancestors of all extant mammals and of all extant amniotes (Diogo et al., 2013). There many clear empirical cases of how forelimb and hind limb muscles that are strikingly similar to each other in our species were actually acquired relatively recently in our evolutionary history, and strikingly often from different muscle primordia and/or at different geological eras, likely due to functional and/or topological constraints exactly as postulated by Lankester (1870) (for details about such cases, see Diogo et al., 2013). As explained by Miyashita and Diogo (2016), this does not only apply to evolution, but also to development: structures that are considered to be serial homologues, such as some of the nerves and blood vessels of the forelimb vs hind limb, are actually different from each other at early stages of ontogeny (Figure 3). These facts have lead us to suggest that the pelvic and pectoral appendage of vertebrates are not evolutionary serial homologues, because they contradict the crucial assumptions of *shared history*—they were not acquired at the same time in vertebrate evolution—and of “ancestral similarity/derived divergence” (Diogo et al., 2013; Diogo et al., 2015; Diogo & Molnar, 2014; Diogo, Murawala, & Tanaka, 2014; Diogo, Nacu, & Tanaka, 2014; Diogo & Tanaka, 2014; Diogo & Wood, 2015; Diogo & Ziermann, 2014, 2015; Diogo, Ziermann, & Linde-Medina, 2015; Diogo, Ziermann, Molnar, Siomava, & Abdala, 2018). In fact, even if the pectoral and pelvic

appendages were eventually more similar in the first gnathostomes having *both* of them, than what is indicated by the antiarch *Parayunnanolepis* described by Zhu, Yu, Choo, Wang, and Jia (2012); see Figure 2), as suggested by Trinajstić, Boisvert, Long, and Johanson (2018), such a similarity would not match at all the strikingly high number of bones and muscles that are so markedly similar in the pectoral vs pelvic appendages of highly derived taxa such as humans (Figure 2). Simply put, in terms of the number of bones and muscles that have clear anatomical correspondents in the other appendage, no early gnathostome can match that what is seen in humans, or in salamander (Figure 2; Diogo et al., 2013). That is, indeed clearly an example of derived evolutionary similarity, of parallelism, as previously indicated—based on non-quantitative skeletal studies—by Owen (1849) and more recently by authors such as Coates and Cohn (1998, 1999).

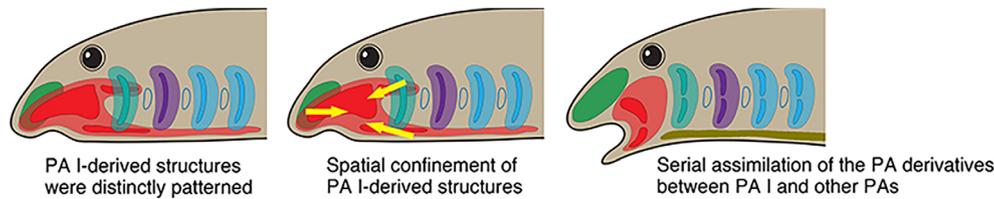
Similar examples of “key emblematic serial homologues” that in reality also became anatomically more alike with time concern the vertebrate branchial arches. This is because the mandibular arch—not only its bones, but also its muscles—is more similar to the other, that is, hyoid and post-hyoid arches in gnathostomes such as sharks than in non-gnathostome vertebrates such as lampreys and hagfishes and in many fossils or early vertebrates (see review by Miyashita & Diogo, 2016). This derived similarity is in fact what lead to the “Mandibular Confinement Hypothesis” of Miyashita (Miyashita & Diogo, 2016), which postulates that a spatial confinement of the “mandibular arch-derived structures” during the evolution of

**FIGURE 3** Development of the arteries of human FL and HL. Modified from Hinchliffe & Johnson (1980; for more details see that book and references therein)

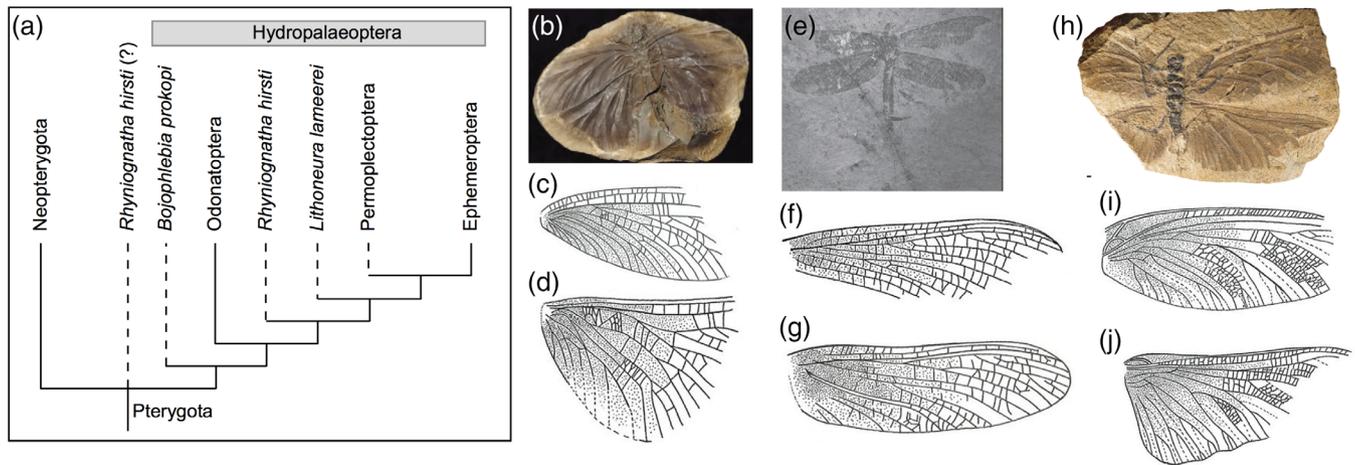


vertebrates, namely during the transitions that lead to the origin of the jaw of gnathostomes, involving a subsequent “serial assimilation” of this arch that resulting in it being more similar to the other branchial arches than is the case in non-gnathostomes (Figure 4).

Taking into account all these observations, as well as the problematic theoretical history of the idea of serial homology, instead of stating that structures such as the pectoral and pelvic appendages are *therefore not* serial homologues because they break crucial a priori



**FIGURE 4** Mandibular Confinement Hypothesis of Miyashita, predicting spatial confinement of the “mandibular arch-derived structures” prior to the origin of the jaw in gnathostomes, with subsequent “serial assimilation” to give rise to an arch that is more similar to the subsequent branchial arches. Modified from Miyashita and Diogo (2016)



**FIGURE 5** Insect forewings and hindwings. (a) Simplified phylogenetic tree illustrating relationships of species and taxa mentioned in the main text. (b) Fossil remains of *L. lameerei* (modified from Grimaldi & Engel, 2005). Illustrations of forewings (c) and hindwings (d) of *L. lameerei* (modified from Carpenter, 1938). (e) Fossil remains of *Triplosoba pulchella* (modified from Prokop & Nel, 2009). Illustrations of forewings (f) and hindwings (g) of *T. pulchella* (modified from Béthoux, 2015). (h) Fossil remains of *Bojophlebia prokopi* (modified from Sroka, Staniczek, & Bechly, 2015). Illustrations of forewings (i) and hindwings (j) of *Bojophlebia prokopi* (modified from Kukalová-Peck, 1985)

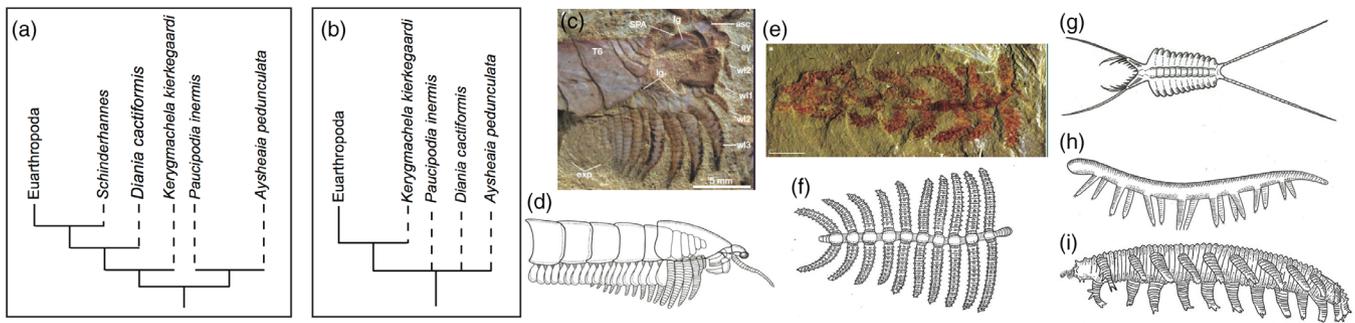
assumptions related to this idea, as we have suggested in our recent studies, in this article, we are instead taking a step back to question whether these assumptions are actually correct at all. Here, we thus review other cases of so-called “emblematic serial-homologues”, such as insect wings, arthropod walking appendages, Dipteran thoracic bristles, and the vertebrae, ribs, teeth, myomeres, feathers, and hairs of chordate animals. Our aim is to contribute to a better understanding—based on empirical data instead of a priori assumptions—of the evolution “serial” structures, and particularly of whether they do reflect cases of ancestral similarity followed by anatomical divergence, or not.

## 2 | SERIAL STRUCTURES

### 2.1 | Insect wings

The origin of wings was a major event in evolution of insects. Powered flight helps them to surmount long distances and facilitates basic tasks such as finding mating partners and food resources (Hedrick, Combes, & Miller, 2015; Searcy & Andersson, 1986). Some derived clades of insects may possess only one functional pair of

wings, while more most insects have two pairs of wings: forewings and hindwings, located on the second and third thoracic segments and often considered to be “serial homologues” (Medved et al., 2015; Monteiro et al., 2007, 2015; Tomoyasu, Ohde, & Clark-Hachtel, 2017). The transition from non-winged insect (apterygots) into winged insects (pterygots) remains unclear. Several hypotheses have been proposed to explain the origin and evolution of wings (e.g., Tomoyasu et al., 2017). An ancient insect that might have had wings was preserved in Pragian Age (411–407 mya; Engel & Grimaldi, 2004). Analysis of mouthparts of *Rhyniognatha hirsti* revealed their morphological similarity to some modern pterygots and the origin of pterygots was assigned to the Early Devonian period (416–397 mya; Figure 5a). Observation of other structures led to a speculation that *R. hirsti* might be a myriapod, not an insect (Haug & Haug, 2017). In any case, the lack of proper wings in the fossil remains of *R. hirsti* makes it unsuitable to answer the key question of the present review and we have to look toward more recent insect lineages. One of such lineages is Mayflies (Ephemeroptera)—the most basal, extant lineage of pterygots (Figure 5a). Modern mayflies comprise only recently evolved lineages, which retain some key features of the stem families (Grimaldi & Engel, 2005). They possess two pairs of wings that do not fold over the abdomen but stay upright, like the wings of butterflies.



**FIGURE 6** Walking appendages of arthropods. (a,b) Simplified phylogenetic trees illustrating relationships of species and taxa mentioned in the main text. (c) Fossil remains of *Chengjiangocaris kunmingensis* (modified from Yang, Ortega-Hernández, Butterfield, & Zhang, 2013). (d) Illustration of *C. kunmingensis* (modified from Yang et al., 2013). (e) Fossil remains of *Diania cactiformis* (modified from Liu et al., 2011a). (f) Illustration of *D. cactiformis* (modified from Liu et al., 2011a). (g) Illustration of *Kerygmachela kierkegaardi* (modified from Budd, 1993). (h) Illustration of *Paucipodia inermis* (modified from Hou, Ma, Zhao, & Bergström, 2004). (i) Illustration of *Aysheaia pedunculata* (modified from Whittington, 1978)

Forewings and hindwings of modern mayflies are clearly heteronomous: they differ in size, shape, and function. Large forewings maintain flight, while reduced hindwings have rather a support function. It has been stated that unlike modern species, basal mayflies had similar forewings and hindwings (Carpenter & Kaesler, 1992; Grimaldi & Engel, 2005; Willmann, 1999). But, what does “similar” mean here?

Wing fossils from mayflies are frequently found in fossil records from the Permian (245–290 mya; Carpenter, 1979; Beckemeyer & Hall, 2007). Remains of the ancient mayfly *Lithoneura lameerei* (Syntonopteridae; Carpenter, 1938) with preserved wings are recorded from the Late Carboniferous (290–310 mya; Edmunds & Traver, 1954; Edmunds, 1975; Wootton, 1981), which makes them approximately 100 mya younger than *R. hirsti*. As other mayflies, *L. lameerei* had two pairs of wings (Figure 5b; Carpenter, 1938). Despite being referred as “similar”, forewings and hindwings appear to be of different size and shape in the fossil photographs (Figure 5b–d). Hindwings are clearly wider than forewings (compare c and d of Figure 5). They expand posterobasally forming a large anal fan (Figure 6d). Wing venation remained a highly debated topic in the past, primarily due to imprecise imprints and uncertainty in the vein nomenclature (Carpenter, 1938; Kukalová-Peck, 1985; Willmann, 1999). Nevertheless, reconstruction of wings illustrates remarkable differences in venation patterns of the forewings and hindwings. Whether they maintained different or identical functions remains unknown.

Two other pterygotes date from a similar geological period: *Triplosoba pulchella* (Triplosobidae; Brongniart, 1983) and *Bojophlebia prokopi* (Bojophlebiidae; Kukalová-Peck, 1985; Figure 5e). *Triplosoba pulchella* is one of the most basal known mayflies (Late Carboniferous [Stephanian], about 300 mya; Figure 5a). It was considered a stem Ephemeroptera until the year 2009, when Prokop and Nel (2009) placed it into the Palaedictyodoptera. Béthoux (2015) revised the species with modern optical techniques and concluded that *T. pulchella* should be returned to the stem Ephemeroptera (Béthoux, 2015). Following this recommendation, in this review, we consider *T. pulchella* as a stem mayfly, one of the earliest known pterygotes. Forewings and hindwings of *T. pulchella* are said to be essentially anatomically similar to each other (Carpenter, 1963;

Wootton & Kukalová-Peck, 2000). However, reconstruction of wings demonstrates certain differences in shape (e.g., enlarged anal part of hindwings) and venation (Figure 5f,g).

The other pterygot species, *B. prokopi* from Czech Republic, was described by Kukalová-Peck (1985) and placed within Ephemeroptera. It was considered the most basal lineage of stem-group mayflies (Grimaldi & Engel, 2005; Rasnitsyn, 2002; Willmann, 2007a, 2007b), until a recent revision of the species (Prokop, Nel, & Tenny, 2010; Staniczek, Bechly, & Godunko, 2011) and its placement as the sister group of all other Hydropalaeoptera (Sroka et al., 2015), more basally than the Lithoneuridae, Triplosobidae, and the whole order Ephemeroptera (Figure 5a). Such positioning makes *B. prokopi* the most basal fossil pterygote with preserved wing records (Figure 5h). Reconstruction of its wings depicts enlarged hindwings with expanded basal and anal parts, which contrast with the narrow forewings, the venation of forewings and hindwings being also markedly different (Figure 5i,j).

## 2.2 | Walking appendages in arthropods

The number of walking appendages varies in modern arthropods. It ranges from three pairs in insects up to 375 pairs in millipedes (*Illacme plenipes*; Marek, Shear, & Bond, 2012). A typical arthropod leg is a jointed appendage, that is, articles (podomeres) consist of hard cylinders of exoskeleton connected by flexible joints between them. Legs of the early euarthropods *Chengjiangocaris kunmingensis* (Yang et al., 2013; Figure 6a,b) are a good example of such morphology. Fossils of *C. kunmingensis* come from the Early Cambrian (550–570 mya; Figure 6c,d). It had twelve pairs of segmented biramous legs, each leg including an exopodit and an endopodit consisting of multiple podomeres. The first two pairs of post-oral limbs are small in size. The third pair is the largest and longest, and the following legs gradually decrease in size toward the cauda (Figure 6c,d). Sclerotization of the body and legs in *C. kunmingensis* indicates a derived phylogenetic position within arthropods. An anatomically more plesiomorphic species could be the worm-like lobopodian *Diania cactiformis* (515–520 mya; Liu et al., 2011a), which as soft body, but bore hard postoral

appendages that morphologically resembled a jointed leg of euarthropods, that is, the mobility of sclerotized limbs was retained by joint-like structures connecting small hard segments (Figure 6e,f). The exact phylogenetic position of *D. cactiformis* remains obscure (Figure 6a, b). Following the two theories of monophyletic versus polyphyletic origin of arthropodized limbs (Legg et al., 2011; Liu et al., 2011a), *Diania* might be placed either within the early arthropods as a sister-group to (*Schinderhannes* + Euarthropoda; Figure 6a; Liu et al., 2011a), or within a paraphyletic grade of lobopodians (Figure 6b) (Legg et al., 2011; Mounce & Wills, 2011). In this article, we review *D. cactiformis* as a remarkable fossil of an early lobopod in the context of homology and similarity of its walking appendages. The imprint and reconstruction of the animal illustrate that its limbs ranged in size, that is, progressively decreased toward the cauda (Figure 6f). The position of limbs relative to the trunk differed between the anterior and posterior ones (Liu et al., 2011a). The angle between anterior limbs 1–4 and the trunk gradually increases from 5 to 40. More posterior limbs (5–10) were placed almost laterally, nearly at right angles. Such a distinction in the orientation of appendages in *D. cactiformis* hints toward the idea that they could perform different tasks (Liu et al., 2011a). In particular, ventral orientation of the anterior limbs makes them more suitable for feeding from the substrate, while posterior limbs might be used for locomotion.

Because the phylogenetic position of *Diania* is not clear, we reviewed other Cambrian-aged lobopodians in order to elaborate whether walking appendages were all similar within the same animal or not. Below, we give details of the three lobopodian species—*Kerygmachela kierkegaardi* (Budd, 1993), *Paucipodia inermis* (Jun-yuan, Gui-qing, & Ramsköld, 1994), and *Aysheaia pedunculata* (Walcott, 1911)—which are basal to *Diania* according to one of the proposed phylogenetic trees (Figure 6a; Liu et al., 2011a, 2011b; Legg et al., 2011). According to the other phylogenetic tree, *Kerygmachela* is the most phylogenetically derived lobopodian among the four reviewed here (Figure 6b; Legg et al., 2011; Mounce & Wills, 2011). *Kerygmachela kierkegaardi* is known from the Early Cambrian (~540 mya). It has sub-triangular non-segmented bulges placed laterally to the body (Figure 6g) that were interpreted as lobopod-like limbs due to their similarity to lobopods in other species, for example, *Aysheaia* (Figure 6i; Budd, 1993). In the reconstruction by Budd (1993), a gradual decrease in the length of the bulges toward the posterior end is depicted. Like in other lobopodians, the length of appendages in *Paucipodia* varies along the anteroposterior axis. Hou et al. (2004) noted that middle lobopods of *P. inermis* are longer and sturdier than those at the head and so-called “tail” (Figure 6h). On the distal tip, each lobopod is supplied with two claws that follow the leg gradient, that is, shorter claws situate on shorter limbs. The lobopods are unequally interspaced: the middle long lobopods are placed more apart, while those at the ends are close together (Hou et al., 2004).

*Aysheaia pedunculata* is likely the most basal stem lobopodian among the ones reviewed here (Figure 6a,b). The caterpillar-shaped body of *Aysheaia* confused the scientific society and it was erroneously placed within fossil annelid worms (Jun-yuan et al., 1994) and then later interpreted as a velvet worm (Onychophora; Liu & Dunlop, 2014). Presently, *Aysheaia* is considered either as a “metataxon” with the

Arthropoda as it appears to possess no currently identified autapomorphies that would allow it to be distinguished from the arthropod crown node (Budd, 2001) or as the sister-group of Arthropoda plus Onychophora (Van Roy, Daley, & Briggs, 2015). It bears ten pairs of not sclerotized limbs with hard claws and spines (Figure 6i). The identification of individual limbs and interpretation of their morphology is obstructed by the fact that soft limbs are often twisted in preservations and overlie the body. Nevertheless, Whittington (1978) noted a gradational increase in length of the anterior limbs (1–3), similarity of the middle limbs (4–7), and a progressive decrease in size toward the tail in posterior limbs (8–10; Liu & Dunlop, 2014, p. 12). Similar to *P. inermis*, limbs of *A. pedunculata* are unequally spaced, that is, posterior limbs (8–10) are progressively closer together. The orientation of the tip claws is different in anterior and posterior appendages: claws on limbs 1–8 point backward, while claws of limbs 9 and 10 point forward.

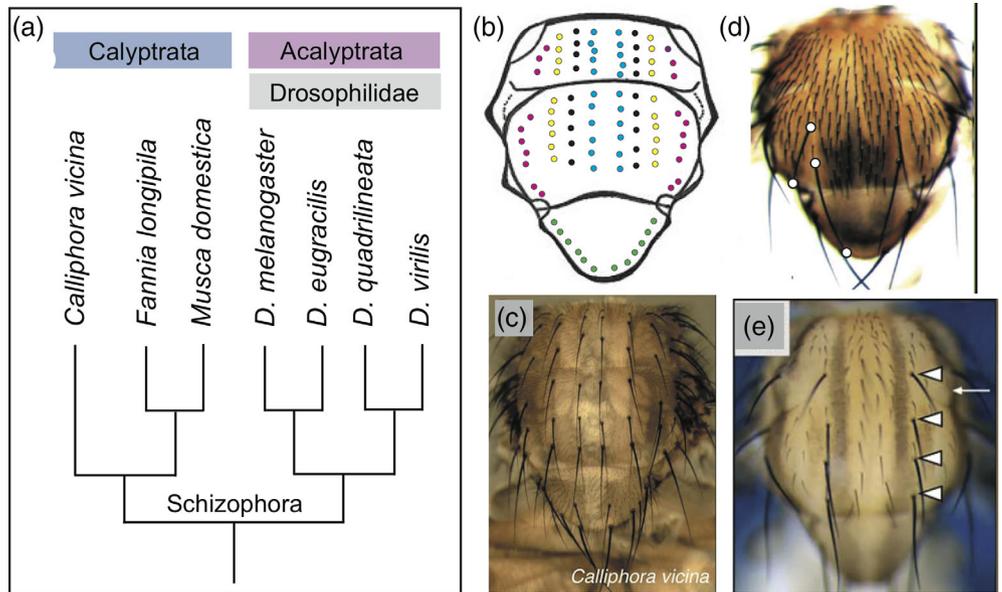
### 2.3 | Thoracic bristles in Diptera

The origin of sensory thoracic bristles in dipteran insects is relatively recent: it has been proposed that the large sensory bristles, macrochaetae, may have arisen in the lineage that led to the Brachycera (McAlpine, 1981). Upon emergence, macrochaetae were arranged in a specific pattern of four longitudinal rows on the scutum, which can be observed in the Schizophora (Figure 7a,b; McAlpine, 1981; Simpson, Woehl, & Usui, 1999), which diverged into two lineages approximately 100 mya: Calypttrata and Acalypttrata (Figure 7a). Calypttrata bears more macrochaetae than Acalypttrata in general, and in particular, many species of Calypttrata retain the stereotyped ancestral bristle pattern (Simpson et al., 1999; compare b and c in Figure 7). For example, *Calliphora vicina* (Family: Calliphoridae) has an ancestral pattern of four complete bristle rows that extend from anterior to posterior in relation to the scutum (Figure 7c; Pistillo et al., 2002). The image in Figure 7c illustrates the difference in size and thickness of the thoracic bristles: in each row, anterior bristles are shorter and thinner than the posterior ones. The same trend is present among dorsocentral bristles of other Calypttrata species, for example, *Fannia longipila* (Family: Fanniidae) and *Musca domestica* (Family: Muscidae; Figure 7a). In the family Drosophilidae, the anterior dorsocentrals are lost in most species (Marcellini & Simpson, 2006). Many extant and extinct *Drosophila* display only two scutellar dorsocentrals for example, *Drosophila melanogaster* (Grimaldi, 1987, 1990; Sturtevant, 1970). In *D. melanogaster*, the anterior dorsocentral bristle is apparently shorter than the posterior one (Figure 7d). Although *D. quadrilineata* regained two additional bristles on the prescutum and possess four dorsocentrals (Marcellini & Simpson, 2006), anterior bristles remain shorter than posterior ones (Figure 7e).

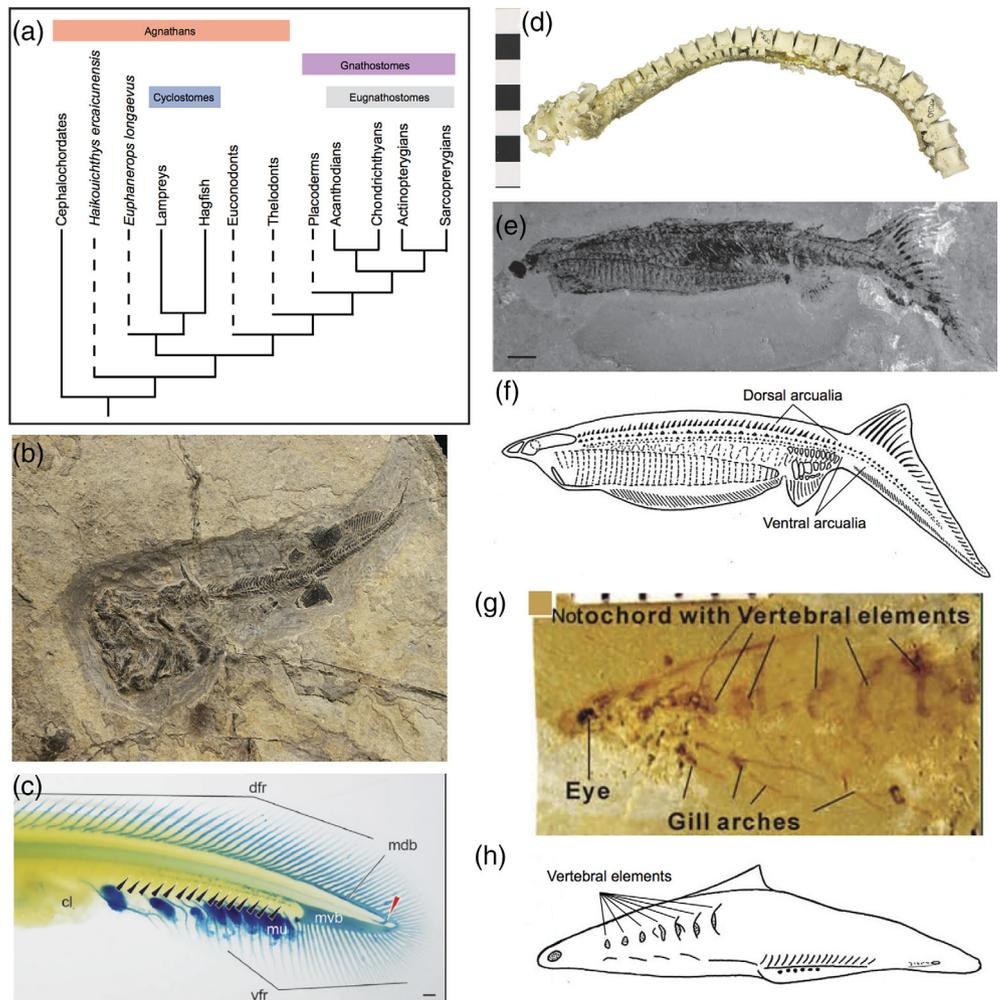
### 2.4 | Vertebrae

The serially repeated vertebrae, composing a “backbone”, were among the first structures to be considered serial homologues (e.g., Filler, 1986; Galis, 2007; Owen, 1848). The two vertebral

**FIGURE 7** Thoracic bristles. (a) Simplified phylogenetic tree illustrating relationships of species and taxa mentioned in the main text. (b) Schema demonstrating ancestral pattern on thoracic bristles in *Schizophora* (modified from Pistillo, Skaer, & Simpson, 2002). (c) Photograph of dorsal thorax of *Calliphora vicina* (modified from Calleja et al., 2002). (d) Dorsal thorax of *Drosophila melanogaster* (modified from Calleja et al., 2002). (e) Dorsal thorax of *Drosophila quadrilineata* (modified from Marcellini & Simpson, 2006)



**FIGURE 8** Vertebrae. (a) Simplified phylogenetic tree illustrating relationships of species and taxa mentioned in the main text. (b) Fossil remains of basal taxon with vertebrae and (c) alcian blue staining of cartilaginous nodules in the tail of the hagfish *Eptatretus burger* (modified from Ota, Fujimoto, Oisi, & Kuratani, 2013). (d) Skeleton of lamprey *Petromyzon marinus* (modified from consulted item of Smithsonian Institution). (e) Fossil remains and (f) illustration of *Euphanerops longaevus* (modified from Janvier & Arsenault, 2007). (g) Fossil remains and (h) illustration of *Haikouichthys ercaicunensis* (modified from Shu, 2003; Shu et al., 2003)



elements, the vertebral body (or centrum) and vertebral arches (dorsal/neural and ventral/haemal), are proposed to arise independently. Vertebral arches might have evolved in ancestral Agnatha and

vertebral centra appeared later within jawed vertebrates (Gnathostomata) once (Fleming, Kishida, Kimmel, & Keynes, 2015) or multiple times (Arratia, Schultze, & Casciotta, 2001; Figure 8a).

Mineralized centra of vertebrae are present in almost all major lineages of Eugnathostoma, while mineralized vertebral arches and non-mineralized centra are found in basal vertebrates, such as armored placoderms (i.e., basal vertebrates belonging to the stem-group of Gnathostomata) and cyclostomes (lampreys and hagfish; Figure 8a). The vertebral column has been studied in three placoderm species, *Ctenurella* (Stensiö, 1963a), *Cocuosteus* (Miles & Westoll, 1968), and *Couralepis* (Ritchie, 2005). Their vertebrae consist of neural and haemal arches, which bifurcate and envelope the notochord and vessels. The size of the arches decreases anteroposteriorly (Figure 8b) and the shape varies in different regions of the backbone, for example, the cervical arches in *Ctenurella*. Anterior vertebrate elements are frequently fused together and form synarcual ossifications, which supports the median dorsal plate of the exoskeleton covering the head and thorax of the animal. Varying numbers of affected vertebrae and degrees of synarcual fusion are known among different placoderms (Long, 1997; Milles & Young, 1977; Stensiö, 1963b). For example, the synarcual of *Couralepis mclachlani* is formed by the fusion of the first four neural arches but the number of involved vertebrae can get up to 20 in other species (Johanson, Carr, & Ritchie, 2010; Ritchie, 2005). At the other end, posterior vertebrae of *C. mclachlani* deepen to support the caudal fin and are supplemented by an additional row of subhaemal elements that extend to the tip of the sharply pointed tail. The distinct morphology of the posterior vertebrae was interpreted to be related to performing a different function (Ritchie, 2005).

Mineralized vertebral arches of placoderms have likely evolved from the endoskeleton of basal jawless fishes that have often mineralized but non-ossified parts of the skeleton (Ota, Oisi, Fujimoto, & Kuratani, 2014). Modern cyclostomes (Figure 8a) have a cartilaginous axial skeleton with irregularly shaped and partially calcified vertebral elements. In extant hagfish, small cartilaginous nodules are positioned ventral to the notochord in a way resembling the axial skeleton of gnathostomes (Ota et al., 2013; Ota, Fujimoto, Oisi, & Kuratani, 2011). The morphology of these nodules was described for the in-shore hagfish *Eptatretus burger* (Ayers & Jackson, 1901), but only recently these structures were shown to be molecularly and developmentally homologous to vertebral elements (Ota et al., 2011, 2013). Localized ventrally, they are reminiscent of haemal arches of other vertebrates. Staining with alcian blue (Figure 8c) highlights the nodules in the postcloacal region of an adult hagfish and illustrates their gradual change in size along the anteroposterior axis. The main axial skeleton of the other group of cyclostomes, the lampreys, consists of a notochord and series of paired cartilaginous vertebrae (arcualia), which are serially repeated on either side along the notochord (Tretjakoff, 1926). Each arcualium consists of the dorsal cartilaginous arch elements, regarded as homologous to the neural arches of gnathostome vertebrae (Gadow, 1933; Goodrich, 1930). We inspected the image of a lamprey skeleton that we identified from the available gallery of the Smithsonian Institution (Frey, n.d.) and found that in that specimen of *Petromyzon marinus* (NC62070) the arcualia gradually increase in size and get more apart toward the tail (Figure 8d).

The two stem jawless species, *Euphanerops longaevus* (~380 mya; Woodward, 1900) and *Haikouichthys ercaicunensis* (~550 mya; Shu

et al., 1999; Xian-guang, Aldridge, Siveter, Siveter, & Xiang-hong, 2002), can shed some light on the origin and evolution of the dorsal arches in lampreys and ventral arches in hagfish (Janvier & Arsenault, 2002). *Euphanerops longaevus* lived in the Devonian and might belong to the stem cyclostomes (Janvier, 2011; Ota et al., 2011; Figure 8a). Extensive calcification of the *E. longaevus* axial skeleton allowed its preservation in fossils (Figure 8e). The skeleton is composed of two parallel series of dorsal and ventral elements of irregular shape organized along the body (Figure 8f). The elements are frequently bifid, and the notochord lies between them. The dorsal elements are generally elongated, posterodorsally tilted, and display a slender dorsal process (Janvier & Arsenault, 2007). They resemble the vertebrae of lampreys (Marinelli & Strenger, 1954, fig. 64). The ventral elements are smaller than the dorsal ones. They have elongated structures that connect them to the elements of the "haemal series", smaller elements situated below the arcualia and enlarged in the caudal region. The connection of ventral elements to other structures implies some degree of specification of the ventral series and possibly functional distinction. Unfortunately, the tail of *E. longaevus* was not preserved in the specimens with mineralized arcualia, so we cannot evaluate their size and whether it changes along the body. However, the reconstruction by Janvier and Arsenault (2007), allows us to assume that arcualia would decrease the size along with the narrowing of the tail (Figure 8f). The other stem-craniate jawless specimen with mineralized vertebral elements, *H. ercaicunensis*, was described by Shu et al. (2003). It has series of separated cartilaginous elements associated with the notochord. Like in *E. longaevus*, individual arcualia of *H. ercaicunensis* are irregular in shape and clearly bifid or arched on their dorsal and ventral sides (Shu, 2003; Shu et al., 2003). Several anterior arcualia decreasing in size toward the head is visible in the preserved specimens and their reconstruction (Figure 8g,h). Other arcualia were either not preserved or hidden by the overlying impressions of the trunk myomeres. However, the caudal region of *H. ercaicunensis* is narrower than the trunk (Figure 8h), suggesting that the notochord in this region is likely thinner and the vertebral elements smaller.

Concerning more derived forms, Filler (1986) wrote a monograph focused specifically on the evolution of vertebrae, particularly in mammals, with a title that relates directly to the issues being discussed in the present paper: "Axial character seriation in mammals—an historical and morphological exploration of the origin, development, use, and current collapse of the homology paradigm". He pointed out that, although there was likely never an animal in which all the vertebrae were similar to each other—as put by Roth (1994). The atlas was likely never similar to the other vertebrae, that is, no true ancestral similarity. One can say, however, that the type of regionalization seen in mammals, such as the lumbar vertebrae being more markedly different from the thoracic ones, is not so obvious in non-mammalian taxa. This idea was supported in a recent study using morphometric data, which has shown that during synapsid evolution there was indeed a general increase of both regionalization and heterogeneity in the spine (Jones et al., 2018). However, Filler (1986) pointed out that if one does a more detailed analysis, that is, comparing not each vertebra as a

whole, but instead each of its subparts, in many cases what appears to be cases of “serial homology”, such as those between the “transverse processes” of the thoracic versus lumbar vertebrae, concerns instead likely cases of derived similarity, that is, they actually derive evolutionary from different structures. For him, this derived similarity might be related to “fields of homology”, that is, like in some taxa that lost the thumb the digit 1 occupies the position of this digit and might therefore also acquire some of its morphological features by occupying its “homeotic identity field”, this might have also lead to the derived similarity of the “transverse processes” of different “types” of vertebrae. What Filler (1986) proposes for the evolution of vertebrae is similar to what Diogo et al. (2013) proposed for the pectoral and pelvic appendages: even if as a whole one of them could eventually be seen as a “repetition” of the other, apart from the fact that were actually never truly ancestrally similar, many of the subparts that compose them, such as their muscles, actually became more similar to each other with time (derived similarity), not the opposite (i.e., no polysomerism followed by anisomerism).

## 2.5 | Ribs

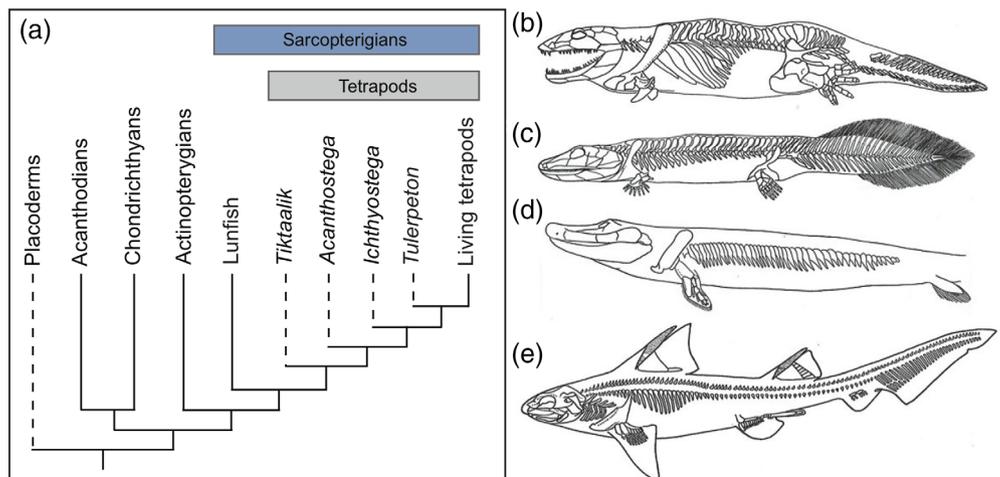
Ribs surround the chest and form a rib cage, which supports and protects the lungs and other inner organs of modern tetrapod animals. The homologies between structures of cartilaginous fishes (Chondrichthyes), including sharks (Figures 8a and 9a), to the ribs of bony fishes and tetrapods has not been fully established. In some influential works, shark ribs are defined as *dorsal* ribs and, thus, considered to be homologous to the ribs of tetrapods (e.g., Compagno, 2001; Goepfert, 1895; Goette, 1879; Goodrich, 1930). Within this scenario, one can say that usually cartilaginous fishes do not have a proper rib cage, having instead short outgrowths that resemble the ribs of Osteichthyes (Kisia, 2010). Some elasmobranchs, such as sawfishes and guitarfishes, have well developed and elongated “dorsal” ribs (Hamlett, 1999). Calcified ribs have also been found in fossils of some ancient sharks (Carroll, 1988; Maisey, 1982). In particular, palaeozoic sharks, such as xenacanth and hybodonts, typically had calcified ribs.

Different hybodont species (e.g., *Hybodus cassangensis*, *H. hauffianus*, *H. fraasi*) had a well-developed rib cage consisting of 10–12 rib pairs differentiated anteroposteriorly (Maisey, 1982). Ribs of ancient sharks were much longer than those of modern elasmobranchs: they were long in the middle and became shorter toward both ends of the ribcage (Figure 9e) (Carroll, 1988; Maisey, 1982). Another extinct shark *Onychoselache traquairi* (Dick & Maisey, 1980) had a similar ribcage morphology, that is, the longer ribs occurred in the middle (Coates & Gess, 2007; Dick & Maisey, 1980). However, it should be noted that other authors defend a different scenario: that sharks possess only *ventral* ribs that are not homologous to the ribs of tetrapods (Kolvekar, Simon, & Kolvekar, 2016; Maisey, 1982). Alternatively, it has been proposed that the ribs of all gnathostomes, including sharks, are ventral and that dorsal ribs do not exist (Britz & Bartsch, 2003).

Therefore, it is important to refer here to bony fishes, in particular to *Polypterus*, which is an extant freshwater fish of the most basal extant group of ray-finned fishes, the Actinopterygii (Figure 9a). Being somewhat phylogenetically close to the common ancestor of Sarcopterygii and Actinopterygii (Inoue, Miya, Tsukamoto, & Nishida, 2003), *Polypterus* is often considered as an extant analogue of stem tetrapods (Standen, Du, & Larsson, 2014). *Polypterus senegalus* possess two sets of ribs: the dorsal and the ventral (pleural) ribs, which attach to the upper and lower parts of the vertebral arches, respectively (Bartsch & Gemballa, 1992; Goodrich, 1930). Dorsal ribs of *Polypterus* (as well as ribs of other fishes) are considered homologous to the ribs of tetrapods (Clack, 2002). The dorsal ribs of adults of *P. senegalus* become shorter and smaller toward the tail (Bartsch & Gemballa, 1992; Goodrich, 1930). They are short in the posterior abdominal region and disappear completely in the tail. Pleural ribs, which are not homologous to tetrapod ribs, are differentiated as well. Posterior pleural ribs are longer than the anterior ones; in the tail, they bend downwards and pass into haemal arches.

The first representatives of early tetrapods diverged from their ancestors in the Early Devonian, approximately 400 mya (Figure 9a; George & Blicek, 2011; Narkiewicz & Narkiewicz, 2015). Two emblematic Devonian tetrapods, that is, *Acanthostega* (Coates, 1996) and *Ichthyostega* (Jarvik, 1996; Ahlberg et al., 2005; Figure 9b,c),

**FIGURE 9** Ribs. (a) Simplified phylogenetic tree illustrating relationships of species and taxa mentioned in the main text. Illustration of (b) *Ichthyostega* and of (c) *Acanthostega* (modified from Ahlberg, Clack, & Blom, 2005). (d) Illustration of *Tiktaalik* (modified from Daeschler, Shubin, & Jenkins, 2006). (e) Illustration of *Hybodus sp.* (modified from Maisey, 1982)



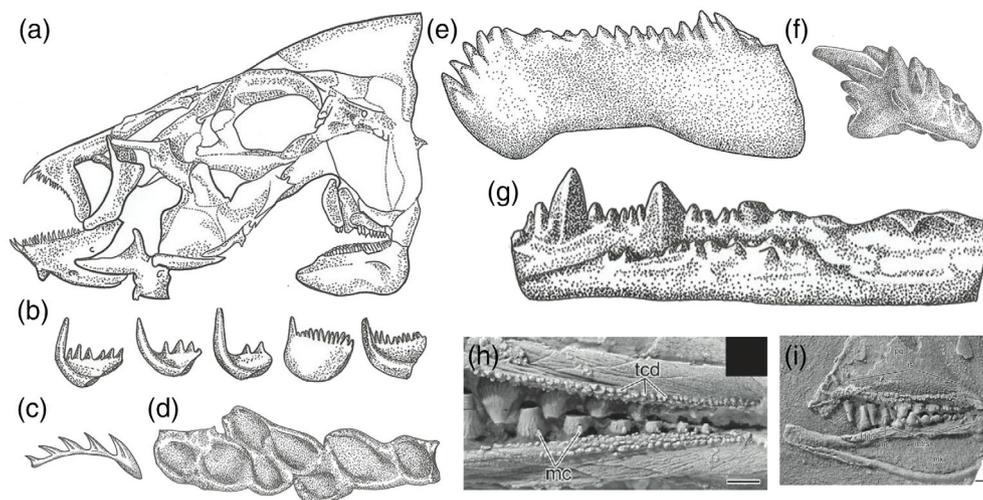
represent the “fish-to-tetrapod” transition and their nearly completely preserved postcranial skeletons show that *Ichthyostega* had a ribcage consisting of cervical, thoracic, and lumbar ribs progressively shorter toward the head and the sacrum (Figure 9b), the sixth and/or seventh thoracic ribs being the longest (Ahlberg et al., 2005). Unlike in *Ichthyostega*, the ribs of *Acanthostega* were not curved ventrally, and their morphology varied along the body axis, that is, the atlantal, axial, and caudal ribs were longer (Figure 9c) (Coates, 1996). The tetrapod-like fish *Tiktaalik roseae* (Sarcopterygii; Daeschler et al., 2006) is ancestral to both *Acanthostega* and *Ichthyostega* (Figure 9a). *Tiktaalik* was semi-aquatic and spent much time in shallow waters and seemingly did not require a fully formed rib cage. However, series of imbricate ribs that decreased in size toward the tail were preserved (Figure 9d). In *Eusthenopteron fordi*, another extinct member of Sarcopterygii, ribs also differed in size and shape (Cote, Carroll, Cloutier, & Bar-Sagi, 2002).

## 2.6 | Teeth

Teeth are present in the mouth of most jawed vertebrates (gnathostomes). Development of the two types of teeth, the oral and the pharyngeal ones (e.g., Koussoulakou et al., 2009), is regulated by the same fundamental genetic network and therefore they are considered serial homologues (Figure 10a; Fraser et al., 2009). Jawless vertebrates (Agnatha) usually do not have teeth, but some of them possess oral denticles, which may or may not be complemented with pharyngeal denticles. These denticles are believed to have evolved independently from the true teeth of jawed vertebrates via co-option of similar genetic networks (Donoghue & Rücklin, 2016; Murdock

et al., 2013). Thus, the remarkable similarity of tooth-like structures of jawed and jawless vertebrates does not imply homology between them, but is rather an example of homoplastic evolution. A basal group of extinct jawless chordates with mineralized oral skeleton is the Euconodonts (Figure 8a), from the Cambrian to the Triassic (Donoghue, Forey, & Aldridge, 2000). A mineralized feeding apparatus located in their oropharyngeal region functioned the teeth-like elements and consisted of enamel-like cap and dentine-like base (Purnell, 1995; Sansom, 1996; Sansom, Smith, & Smith, 1994; Smith, Sansom, & Smith, 1996). Different types of teeth-like elements differed in radii of curvature and the number of denticles along the posterior margin (Figure 10b). Such gradient in morphology was proposed to occur due to a tight control of polarity and shape gradient during development (Smith & Coates, 1998). Thelodonts represent another group of jawless fishes (Figure 8a) with oral skeleton, formed by oropharyngeal scales of various shapes (Bruggen, 1992; Bruggen & Janvier, 1993; Märss, 1986). For example, whorl-like arrays of jointed denticles were present in the naso-oropharyngeal cavity of *Loganellia scotica* (430–370 mya) (Figure 10c; Bruggen & Janvier, 1993). Size and shape of thorns in the whorl-like elements gradually change along the curvature. The internal scales grew to different sizes (Figure 10d). They were polarized: all denticles were aligned in parallel and their cups headed same direction (Smith & Coates, 1998, 2000). In another genus of thelodonts, *Phlebolepis*, oral denticles also form a gradient of different shapes: *P. elegans* have denticles shaped from rhomboid to round and *P. ornate* from round to oval (Märss, 1986).

The most ancient jawed vertebrates with true teeth are the placoderms (Smith & Johanson, 2003; Johanson & Smith, 2005; Rücklin et al., 2012; Figure 8a). Homology of placoderm teeth and the teeth of crown gnathostomes has been questioned for a long time



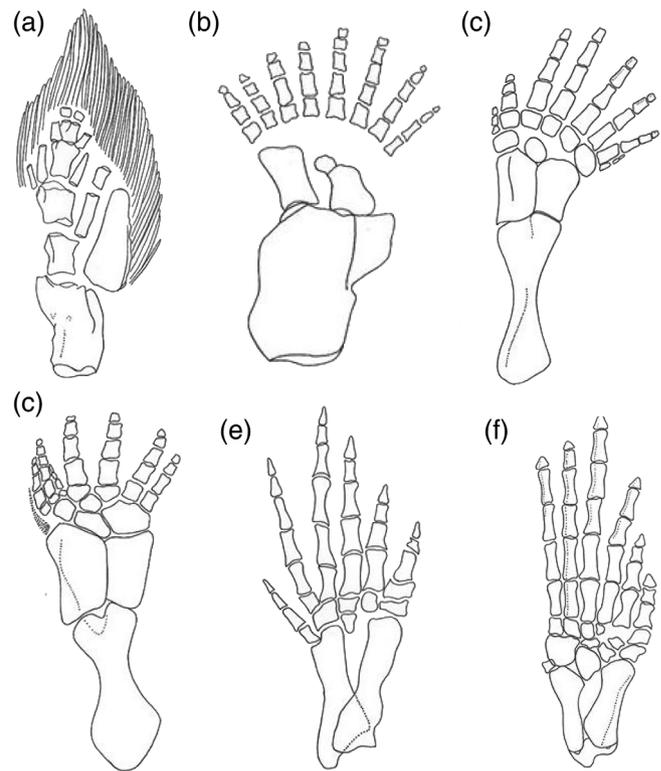
**FIGURE 10** Teeth. (a) Schematic drawing of the generalized cichlid cranial skeleton, showing the oral and pharyngeal teeth (modified from Fraser et al., 2009). (b) Illustration of anteroposterior series of teeth-like elements in *Plegagnathus* (modified from Smith & Coates, 1998). (c) Illustration of whorl-like denticles from the naso-oropharyngeal cavity and (d) of internal scales of *Loganellia scotica* (modified from Smith & Coates, 1998; Donoghue & Rücklin, 2016). (e) Illustration of the lower jaw element of *Compagopiscis croucheri* (modified from Rücklin et al., 2012). (f) Illustration of denticulated plate with tooth whorl of an acanthodian (modified from Burrow, 1995). (g) Illustration of jaw and teeth of *Nostolepis* sp. (modified from Ørving, 1967). (h) Lingual denticles and posterior teeth of *Euryacanthus rugosus* (modified from Blais, Hermus, & Wilson, 2015). (i) Teeth of *Tricuspicanthus gannitus* (modified from Blais et al., 2015)

(Johanson & Smith, 2003, 2005; Ørvig, 1980; Smith & Johanson, 2003). Modern methods of tomographic microscopy showed that distinct teeth of arthropods *Compagopiscis croucheri* (Placodermi) were made of dentine and bone and possessed a pulp cavity (Rücklin et al., 2012). Based on the close resemblance of the structure and morphology of teeth, it has been proposed that placoderm teeth originated within the gnathostome stem lineage and were homologous to the teeth of crown gnathostomes (Rücklin et al., 2012). An example of homodont and conical in shape teeth with a gradual change in size is shown in Figure 10e.

Because the hypothesis of homology of placoderm teeth and teeth of crown gnathostomes is primarily based on their morphological appearance, it has not been fully accepted in the scientific community and some debates are still going on (Burrow, Hu, & Young, 2016; Young, 2003). Therefore, we will refer to fossil species of the acanthodians, or “spiny sharks” (Figure 8a), which represent basal jawed vertebrates and provide insight into the early stages of evolution of crown gnathostomes (Giles, Friedman, & Brazeau, 2015; Rücklin, Giles, Janvier, & Donoghue, 2011). Acanthodians have jaws armored with teeth and tooth whorls, which can be replaced with new teeth. A typical acanthodian tooth whorl is composed of a spirally curved bony base with several rows of odontodes (Figure 10f). There are two types of odontodes, that is, small secondary teeth are organized in side rows (side cusps) and surround the main row of teeth (main cusps), which gradually decrease in size (Burrow, 1995; Gross, 1971). Teeth of the acanthodian *Nostolepis* sp. from the Upper Silurian (416–443 mya) are clearly of different size and morphology (Figure 10g) (Ørvig, 1967). Teeth of other acanthodian species (e.g., *Tricuspicanthus gannitus* and *Erymnacanthus clivus*) also vary in shape and decrease in size posteriorly (Figure 10h,i; Blais et al., 2015).

## 2.7 | Digits

Digit-bearing limbs of early tetrapods evolved in the Devonian period (~350–420 mya), and had more than five digits (e.g., Saxena, Towers, & Cooper, 2017; Ahlberg, 2019; Figures 9a and 11a). *Acanthostega gunnari* had eight digits on each forelimb and hindlimb (Coates & Clack, 1990; Coates, 1996; Figure 11b,c). The anterior and posterior digits of the forelimb had fewer phalanges than the middle ones and were shorter (Figure 11b). In particular, the first four (1–4) and the last (8) digits on the forelimb consisted of three phalanges, while the middle digits (5–7) had four phalanges (Coates, 1996). The second proximal phalanx was longer in digit 3 than in the adjacent digits, while digit 8 was slenderer than the short anterior digits 1 to 3, with the same number of phalanges. The first (1) and the last (8) digits of the hind limb were reduced in size as well (Figure 11c). The number of phalanges in the hind limb digits varied from one in the first digit (1) to three in the middle ones (3–7). *Ichthyostega stensioei* (Save-Soderbergh, 1932), more adapted to a terrestrial life, had seven digits on each hind limb (Coates & Clack, 1990; Ahlberg, 1996; Saxena et al., 2017; Figure 11d). The first three digits (1–3) were positioned close together and composed of three, four, and two phalanges, respectively (Coates &



**FIGURE 11** Digits. (a) Illustration of fins of *Tiktaalik* (modified from Shubin, Daeschler, & Jenkins, 2006). Illustrations of (b) forelimb and (c) hind limb of *Acanthostega* (modified from Coates, 1996). Illustration of (d) hind limb of *Ichthyostega* (modified from Coates & Clack, 1990). Illustrations of (e) forelimb and (f) hind limb of *Tulerpeton* (modified from Lebedev & Coates, 1995)

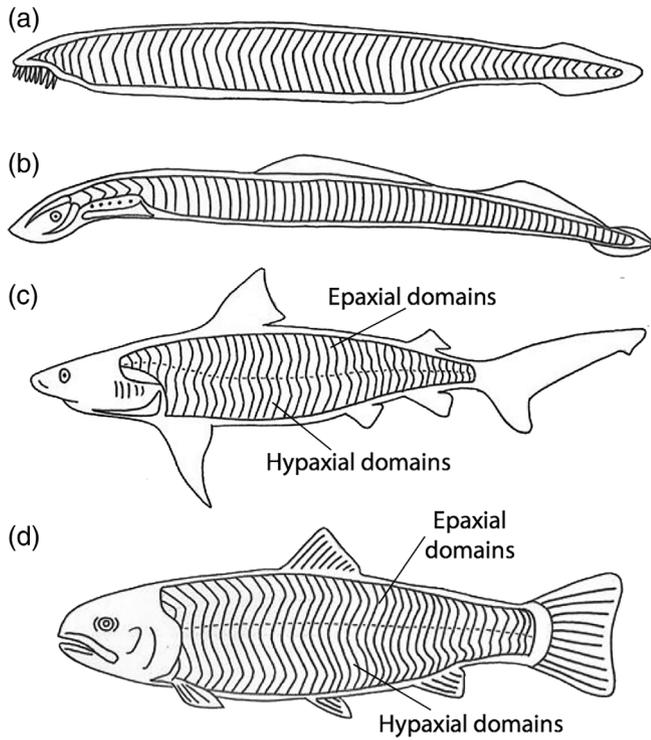
Clack, 1990). The other four digits (4–7) were spread apart, and composed of three to four phalanges. The number of digits on the forelimb of *Ichthyostega* remains unknown. *Tulerpeton curtum* (Lebedev, 1984) had six digits on each limb (Figure 11e,f), the number of phalanges, and the size of these digits gradually decreasing from the middle to the anterior and posterior ends (Lebedev & Coates, 1995).

## 2.8 | Myomeres

Serial segments of axial muscles (myomeres) can be traced back to ancestral invertebrate chordates (Delsuc, Tsagkogeorga, Lartillot, & Philippe, 2008; Putnam et al., 2008). In the basal cephalochordates, as well as in vertebrate fishes (Figure 11a), myomeres form series of vertical strips (Figure 12a–d) that allow swimming in an undulatory manner (Liem & Walker, 2001). In gnathostomes, the myomeres are subdivided by a horizontal myoseptum into two domains, the dorsal (epaxial) and the ventral (hypaxial; Figure 12c,d; Goodrich, 1930). In basal extant vertebrates, such as lampreys, and in cephalochordates this distinction is absent (Kusakabe & Kuratani, 2005) (Figure 12a,b). In acrania and vertebrates, each myomere consists of muscle fibers with different functional capabilities (Bone, 1989; Kusakabe & Kuratani, 2005; Lacalli & Kelly, 1999). Fast (or deep) muscle fibers are

responsible for rapid burst swimming and escaping from predators. Slow (or superficial) fibers allow prolonged but slow swimming.

Concerning fossil taxa, the composite camera lucida drawings of the extinct chordate *Haikouichthys ercaicunensis* (Shu et al., 1999;

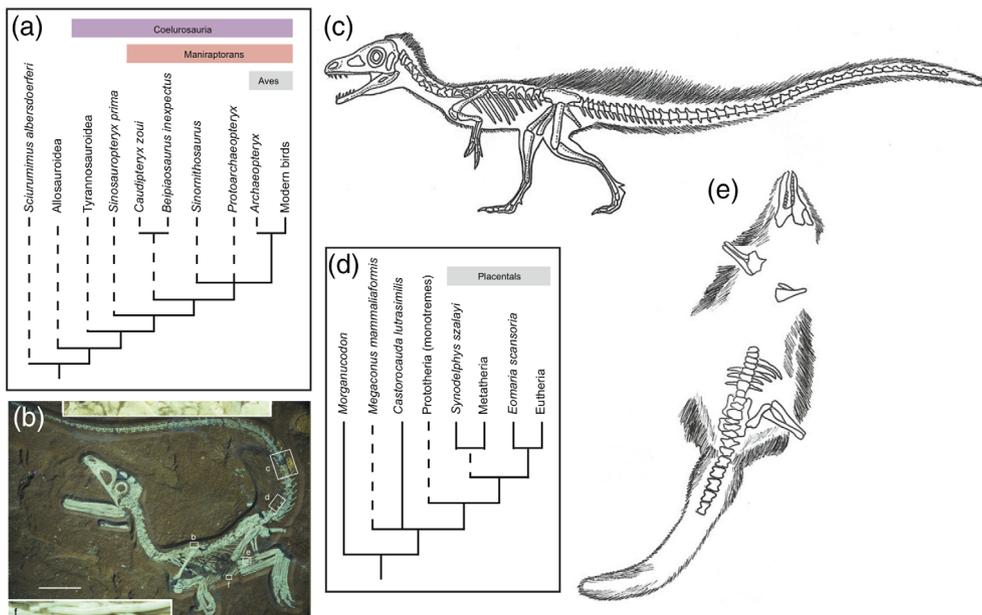


**FIGURE 12** Myomeres. Illustrations of myomeres in a (a) lancelet, (b) lamprey, (c) cartilaginous, and (d) bony fish; (e) Camera lucida drawings of *Haikouichthys ercaicunensis* illustrating myomeres (modified from Xian-guang et al., 2002). (f) Backscattered scanning electron micrograph of *Pikaia gracilens* (modified from Morris & Caron, 2012)

Xian-guang et al., 2002) from the Low Cambrian (~550 mya; Figure 8a) illustrates myomeres unevenly distributed along the body axis. Myomeres seem to be denser in the trunk and caudal region than in the front part. Their size and shape gradually change along with the body, and caudal myomeres are more steeply inclined than the anterior ones (Lacalli, 2012). Basal to *Haikouichthys* is *Pikaia gracilens* (Walcott, 1911), known from fossil remains of the Middle Cambrian. Due to the presence of numerous sigmoidal myomeres, *P. gracilens* has been classified as a stem chordate (Morris & Caron, 2012) or as basal members of the chordate lineage (Lacalli, 2012). Myomeres in *P. gracilens* resemble slow muscle fibers in fishes. Although they look somehow uniform superficially, the anterior myomeres were described as more simple, and more circular, by Morris and Caron (2012), the 10–15 segments at the anterior and posterior ends of the body being denser than the middle ones.

**2.9 | Feathers**

Scales, feathers, and hair are epidermal derivatives that are broadly characteristic of non-avian sauropsids, birds, and mammals, respectively. Their origin, links, and evolution remain widely discussed (e.g., Alibardi, 2003; Bergman, 2003; Di-Poï & Milinkovitch, 2016; Eckhart et al., 2008; International Chicken Genome Sequencing Consortium, 2004; Maderson, 1972, 2003; Musser, Wagner, & Prum, 2015; Zimek & Weber, 2005). It has been proposed that the complex asymmetric feathers of *Archaeopteryx*, resembling feathers of modern birds, evolved from proto-feathers, which, in turn, originated from hollow tubular integumentary filaments of early non-avian dinosaurs (Chen et al., 2015; Prum, 1999; Unwin, 1998). The idea that these simple filaments represent an intermediate evolutionary stage toward more complex feathers is still under debate (reviewed in Unwin, 1998).



**FIGURE 13** Scale derivatives. (a,d) Simplified phylogenetic trees illustrating relationships of species and taxa mentioned in the discussions about feathers and hairs. (b,c) concerns the plumage of *Sciuromimus albersdoerferi* (modified from Rauhut et al., 2012; www.dinosaurpictures.org). (e) Illustration of *Castorocauda lutrasimilis* (modified from Ji, 2006)

**TABLE 1** Description of the main differences between serial structures reviewed in this article

Serial structure	Taxa	Species	Difference
Wings	Ephemeroptera	<i>Lithoneura lameerei</i>	(a) Size and shape variation: AP gradient and (b) variation in venation
		<i>Triplosoba pulchella</i>	(a) Size and shape variation: AP gradient and (b) variation in venation
		<i>Bojophlebia prokopi</i>	(a) Size and shape variation: AP gradient and (b) variation in venation
Walking appendages in arthropods	Lobopodians	<i>Aysheaia pedunculata</i>	(a) Size variation: AP gradient, (b) un-equal spacing of limbs and possibly (d) differentiation in function
		<i>Paucipodia inermis</i>	(a) Size and shape variation: AP gradient; un-equal spacing of limbs
		<i>Kerygmachela kierkegaardi</i>	(a) Size variation: AP gradient
		<i>Diania cactiformis</i>	(a) Size variation: AP gradient and (d) differentiation in function
	Euarthropods	<i>Chengjiangocaris kunmingensis</i>	(a) Size variation: AP gradient and (b) short two anterior pairs
Thoracic bristles in Diptera	Calyptrata	<i>Calliphora vicina</i>	(a) Size variation: AP gradient
		<i>Fannia longipila</i>	(a) Size variation: AP gradient
		<i>Musca domestica</i>	(a) Size variation: AP gradient
	Acalyptrata	<i>Drosophila melanogaster</i>	(a) Size variation: AP gradient
		<i>Drosophila quadrilineata</i>	(a) Size variation: AP gradient
Vertebrae	Stem cyclostomes	<i>Haikouichthys ercaicunensis</i>	(a) Size variation: AP gradient
		<i>Euphanerops longaevus</i>	(a) Size variation: AP gradient
	Lampreys	<i>Petromyzon marinus</i>	(a) Size variation: AP gradient
	Hagfish	<i>Eptatretus burger</i>	(a) Size variation: AP gradient
	Placoderms	<i>Couralepis mclachlani</i>	(a) Size variation: AP gradient and (d) regionalization in synarcual and posterior vertebrae supporting the caudal fin
		<i>Ctenurella</i>	(a) Size variation: AP gradient and (d) regionalization in cervical arches
Ribs	Chondrichthyes	<i>Hybodus</i>	(a) Size variation: AP gradient
	Actinopterygii	<i>Polypterus</i>	(a) Size variation: AP gradient and (b) posterior ribs bend downwards
	Sarcopterygii	<i>Eusthenopteron foordi</i>	(a) Size variation: AP gradient
		<i>Tiktaalik roseae</i>	(a) Size variation: AP gradient
	Tetrapoda	<i>Acanthostega</i>	(a) Size variation: AP gradient
<i>Ichthyostega</i>		(a) Size and shape variation: AP gradient	
Teeth	Euconodonta	-	(a) Size and shape variation: AP gradient, (b) big anterior tooth and (d) different types and number of denticles
	Thelodonta	<i>Loganellia scotica</i>	(a) Size and shape variation in a gradient and (d) different types
		<i>Phlebolepis</i>	(a) Shape variation in gradients
	Placodermi	<i>Compagopiscis croucheri</i>	(a) Size and shape variation: PD gradient
	Acanthodii	<i>Nostolepis sp.</i>	(a) Size and shape variation: PD gradient and (d) different types
		<i>Tricuspicanthus gannitus</i>	(a) Size and shape variation: PD gradient
		<i>Erymnacanthus clivus</i>	(a) Size and shape variation: PD gradient

(Continues)

TABLE 1 (Continued)

Serial structure	Taxa	Species	Difference
Digits	Tetrapoda	<i>Ancathostega gunnari</i>	(a) Size and shape variation: AP gradient and (c) digits 5–7 have extra one, fourth phalanx; the second proximal phalanx is longer in the digit 3
		<i>Ichthyostega stensioei</i>	(a) Size and shape variation: AP gradient; variation in the number of phalanges and (b) digits 1–3 close together while others are apart
		<i>Tulerpeton curtum</i>	(a) Size and shape variation: AP gradient; variation in the number of digits
Myomeres	Chordata	<i>Pikaia gracilens</i>	(a) Variation in size, shape, and density: AP gradient
		<i>Haikouichthys ercaicunensis</i>	(a) Variation in steepness, shape, and density: AP gradient
		<i>Amphioxus</i>	(d) Two types
Hair	Mammalia	<i>Megaconus mammaliaformis</i>	(a) Variation in size in a gradient and (d) two types
		<i>Castorocauda lutrasimilis</i>	(a) Variation in size in a gradient and (d) two types
		<i>Eomaria scansoria</i>	(a) Variation in size in a gradient and (d) two types
		<i>Synodelphys szalayi</i>	(a) Variation in size in a gradient and (d) two types
Feathers	Megalosauridae	<i>Sciurumimus albersdoerferi</i>	(a) Variation in size: DV gradient and possibly (d) two types
	Theropoda	<i>Sinosauropteryx prima</i>	(a) Variation in size: AP and DV gradients and possibly (d) two types
		<i>Beipiaosaurus inexpectus</i>	(a) Variation in size in a gradient and (d) two types
		<i>Caudipteryx zoui</i>	(d) Many types
		<i>Protarchaeopteryx robusta</i>	(d) Many types

The phylogenetically most basal theropod with preserved direct evidence of filamentous plumage is *Sciurumimus albersdoerferi* (Megalosauridae) from the Late Jurassic (~150 mya; Rauhut, Foth, Tischlinger, & Norell, 2012; Figure 13a). Its plumage consisted of two types of non-branching, monofilaments that correspond to type 1 feathers (Prum & Brush, 2002; Xu & Guo, 2009). Long and thick filaments were preserved in the dorsal region of the tail; fine and thin filaments covered the ventral lateral tail flank and ventral part of the body (Figure 13b,c). In the theropod *Sinosauropteryx prima* (Compsognathidae) from the Latest Jurassic/Early Cretaceous (~145 mya), the skull, neck, back, hips, and tail were also covered with filament-like integumentary structures (Chen, Dong, & Zhen, 1998) that, after long debates, were shown to be likely feather homologues (Lingham-Soliar, 2011; Smithwick et al., 2017a, 2017b; Unwin, 1998). Two specimens with plumage were preserved and described—a small one and a large one. In the small specimen, the length of filaments ranged from 5.5 mm in the rostral region to 21 mm at the distal ends of the scapulae. Filaments were of a constant length along the back and decreased to 16 mm dorsal to the ilium. The longest filaments were found above the base of the tail, ventral filaments of the tail were shorter. In the large specimen, the plumage was longer in general, but

reflected the pattern of the small specimen, for example, the longest filaments (about 40 mm) covered the caudal region. In another theropod of a similar age, *Beipiaosaurus inexpectus* (Maniraptora; ~100–145 mya; Figure 13a), the integument consisted of elongated broad filamentous feathers and branched filaments (stage 3–4 by Prum & Brush, 2002) that vary in length from about 50 mm to 70 mm (Chen et al., 2015; Xu, Tang, & Wang, 1999). *Caudipteryx zoui* and *Protarchaeopteryx robusta* from the Late Jurassic to Early period Cretaceous (~145 mya) represent an intermediate form in the evolution of birds from feathered bipedal dinosaurs (Figure 13a). They possessed two types of feathers: cover feathers of wings and tail and downy feathers covering the rest of body (Chen et al., 2015; Qiang, Currie, Norell, & Shu-An, 1998). Differentiated bilaterally symmetrical plumulaceous feathers likely made them capable of flight (Qiang et al., 1998).

## 2.10 | Hair

Because hairs are only found in mammals, they have likely evolved in the synapsid lineage, after the split from sauropsids in the Late Carboniferous approximately 310–330 mya (Donoghue & Benton, 2007;

Kemp, 1982; Rowe, 1988). Hairs are composed of soft tissues, which quickly decay and often leave no trace in fossils. The earlier hair-like structures were found in coprolites (fossil faeces) of carnivorous species from the Latest Permian period, which is ~240 mya (Bajdek et al., 2016). This finding suggests that therapsid synapsids of that period already had hair-like integument. Unfortunately, from these fossil remains it is not possible to infer whether all hairs of the victim's fur were identical, or not. The most ancient fossil remains allowing us to do so are those of *Megaconus mammaliaformis* (Zhou, Wu, Martin, & Luo, 2013) and *Castorocauda lutrasimilis* (Ji, 2006) from the Middle Jurassic approximately 160–165 mya (Figure 13d). These animals were preserved with hair imprints, in which guard hair can be distinguished from carbonized underhairs (*C. lutrasimilis* in Figure 13e), and hairs of different parts of the body have different sizes. The pelage of more advanced animals such as the placental mammal *Eomaria scansoria* (Ji et al., 2002) and boreosphenidan mammal *Synodelphys szalayi* (both 125 mya) (Luo, 2003) also consisted of two types of hair, the guard hairs and dense underfur. It is likely that the appearance and diverse function of hair in modern animals is similar to those of ancestral forms, as the main function of the bottom wool layer is thermoregulation (Wacker, McAllan, Körtner, & Geiser, 2016). Long and generally coarse guard hair protects the undercoat and skin from external negative factors and provides pigmentation and camouflage (Wacker et al., 2016).

### 3 | SUMMARY OF ALL CASE-STUDIES

Tables 1–3 provide a detailed summary of all examples reviewed, and allow us to address the broader questions mentioned in the Introduction. Basically, as highlighted in Table 1, there is always some degree of variation within the “serial” structures within a single individual, even in the phylogenetically most basal taxa where those structures were found. This is particularly the case concerning “serial structures” that are lower in number and/or not sequentially adjacent to each other, such as wings or digits. But even in those cases of “serial structures” that are higher in number and/or more sequential, such as vertebrae, most of them still vary markedly in size and shape in a gradient-dependant manner along the anteroposterior axis of the animal. Moreover, some serial structures exhibit crucial morphological and/or functional differentiation in basal taxa, for example, the walking appendages of arthropods, or the hairs and digits of tetrapods—the clearly different number of phalanges of the digits of early tetrapods being an emblematic example of this. Apart from this lack of true polysomerism in phylogenetically basal taxa, Minelli (2003) pointed out that the study of such structures also rejects the paradigm that numerous serially repeated similar parts—polysomerism—often give rise to fewer and/or more differentiated parts—anisomerism. As noted by him, polychaetes of the family Eucinidae display a highly derived configuration with up to 1,500 body segments, some derived vertebrates such as eels and snakes have more than 300 vertebrae, and some invertebrates such as centipedes and millipedes display a highly derived condition with a huge number of segments with legs. All these

**TABLE 2** Evolutionary trends of serial structures discussed in this article

Evolutionary trends	
(a) Anisomerism (become increasingly more patterned/different)	<ul style="list-style-type: none"> <li>Increasing variation in wing size and shape; modification into haltere or elytra.</li> <li>Appearing of the leg segmentation; modifications into chelas (claws), forcipules, natatorial legs, and so on.</li> <li>Differentiation into cervical, thoracic, lumbar, sacral vertebrae, and coccyx in humans and other vertebrates.</li> <li>Variation in size of vertebrae remains; appearance of cervical and floating ribs.</li> <li>Development of heterodonty, differentiation into incisors, canines, premolars, and molars in humans and other animals.</li> <li>Development of muscles of different size, shape, morphology, and function.</li> <li>Development of vaned and down feathers; differentiation into contour feathers, semiplume and filoplume feathers, and so on.</li> </ul>
(b) Similar levels of pattern complexity	<ul style="list-style-type: none"> <li>The structure and morphology of thoracic bristles remain the same, changes only the pattern: presence/absence.</li> <li>Two types of hair remain in most modern mammals.</li> </ul>
(c) Polysomerism (become less patterned and increasingly uniform)	<ul style="list-style-type: none"> <li>Less variation in the length of digits and number of phalanges</li> <li>Derived similarity between “transverse processes” of lumbar and thoracic vertebrae of mammals</li> </ul> <p>*Plus, from our previous works, as discussed in the Introduction:</p> <ul style="list-style-type: none"> <li>Higher number of pectoral appendage bones and muscles with clear anatomical correspondence in the pelvic appendage</li> <li>Mandibular arch more similar to other branchial arches in sharks than in many extant and extinct jawless vertebrates</li> </ul>

cases indeed reject “Williston's rule” (e.g., Williston, 1914, 1925), according to which there is a general trend in evolution toward a reduction/differentiation in the number of individual serial parts.

These examples those reviewed by us, and the examples concerning the pectoral and pelvic appendages as well as the branchial arches of vertebrates referred to in the introduction, suggest that

**TABLE 3** Evolutionary patterns of serial structures discussed in this paper

Evolutionary patterns	
(a) Size and/or shape variation in a gradient, without major steps	Walking appendages in arthropods (myriapods, insects, spiders) Thoracic bristles in Diptera Ribs (1–10) Digits (2–5) Hair (dogs) Feathers (body and leg feathers)
(b) Singularity of one or a few elements at one end of the series, or both	Walking appendages in arthropods (crabs) Ribs (cervical and floating ribs)
(c) Deviation from the norm of one or very few non-terminal elements, whereas posterior (or distal) elements remain identical to the anterior (or more proximal) ones	Digits (opposed thumb)
(d) Regionalization (tagmatization)	Wings <sup>a</sup> (modern Mayflies) Walking appendages in arthropods (crayfish) Vertebrae (cervical, thoracic, lumbar, sacral vertebrae, and coccyx) Teeth (incisors, canines, premolars, and molars) Myomeres (development of different groups of muscles; myocardium, smooth, and skeletal muscles) Hair (mane of a lion, pony tail, spines of a porcupine) Feathers (wings, body, and tail feathers)

<sup>a</sup>To some extent, as it is not possible to distinguish terminal and non-terminal elements in a series of two elements).

during evolution “serial” structures can either become more different (anisomerism), more similar (polysomerism), or remaining at the same level of similarity (e.g., Table 2). The evolutionary patterns that allow such changes are summarized in Table 3. They include (a) size and/or shape variation in a gradient, without major steps; (b) singularity of one or a few elements at one end of the series, or both; (c) deviation from the norm of one or few non-terminal elements, whereas posterior (or distal) elements remain identical to the anterior (or more proximal) ones; and (d) regionalization (tagmatization).

## 4 | CONCLUSIONS

1. Concerning the assumption of ancestral polysomerism, there are almost never cases of true ancestral similarity, not even in those cases where there is a higher number of “serial” structures, such as the vertebrae, there are always at least some differences between these structures, and is not only a difference of gradation, it also

concerns, for example, the angles and overall anatomy of the legs and other features.

- Concerning the assumption of derived anisomerism, in evolution, “serial” structures such as the vertebra and/or their subparts like the “transverse processes”, many times display trends toward less similarity, for instance when one compares *each* vertebra in non-amniotes versus in mammals.
- In contrast, in many other cases “serial structures” display trends toward more similarity, for instance, the “lumbar versus thoracic transverse processes”.
- In summary, one cannot say that there is a clear, overall trend toward anisomerism.

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## CONFLICT OF INTEREST

None of the authors has any conflict of interest.

## AUTHOR CONTRIBUTIONS

**Natalia Siomava:** Data curation; formal analysis; investigation; methodology; visualization; writing-original draft; writing-review and editing. **Jose Fuentes:** Methodology; validation; visualization; writing-review and editing. **Rui Diogo:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; supervision; validation; writing-review and editing.

## DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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