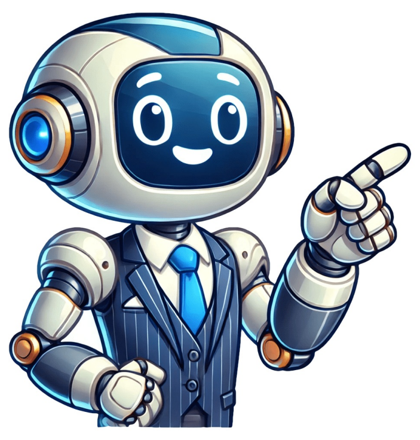
Click to prove
you're human



Akam M (2000) Arthropods: developmental diversity within a (super) phylum. Proc Natl Acad Sci USA 97:4438–4441PubMed CAS Google Scholar Alwes F, Scholtz G (2004) Cleavage and gastrulation of the euphausiacean Meganyctiphanes norvegica (Crustacea, Malacostraca). Zoomorphology 123:125–137 Google Scholar Alwes F, Scholtz G (2006) Stages and other aspects of the embryology of the parthenogenetic Marmorkrebs (Decapoda, Reptantia, Astacida). Dev Genes Evol 216:169–184PubMed Google Scholar Amma K (1911) Über die Differenzierung der Keimbahnzellen bei den Copepoden. Arch Zellforsch 6:497–576 Google Scholar Anderson DT (1965) Embryonic and larval development and segment formation in Ibla quadrivalvis (Cuv.). Austr J Zool 13:1–15 Google Scholar Anderson DT (1966) The comparative early embryology of the Oligochaeta, Hirudinea and Onychophora. Proc Linn Soc New South Wales 91:10–43 Google Scholar Anderson DT (1969) On the embryology of the cirripede crustaceans Tetraclita rosea (Krauss), Tetraclita purpurascens (Wood), Chthamalus antennatus Darwin and Chamaesipho columna (Spengler) and some considerations of crustacean phylogenetic relationships. Phil Trans R Soc B 256:183–235 Google Scholar Anderson DT (1973) Embryology and Phylogeny in Annelids and Arthropods. Pergamon, Oxford Google Scholar Barnett AA, Thomas RH (2012) The delineation of the fourth walking leg segment is temporally linked to posterior segmentation in the mite Archegozetes longisetosus (Acari: Oribatida, Trhypochthoniidae). Evol Dev 14:383–392PubMed CAS Google Scholar Benesch R (1969) Zur Ontogenie und Morphologie von Artemia salina L. Zool Jb Anat 86:307–458 Google Scholar Bergh RS (1893) Beiträge zur Embryologie der Crustaceen. I. Zur Bildungsgeschichte des Keimstreifens von Mysis. Zool Jb Anat 6:491–528 Google Scholar Biffis C, Alwes F, Scholtz G (2009) Cleavage and gastrulation of the dendrobranchiate shrimp Penaeus monodon (Crustacea, Malacostraca, Decapoda). Arthropod Struct Dev 38:527–540PubMed Google Scholar Bigelow MA (1902) The early development of Lepas. A study of cell lineage and germ layers. Bull Mus Comp Zool Harvard 40:61–144 Google Scholar Bock E (1942) Wechselbeziehungen zwischen den Keimblättern bei der Organbildung von Chrysopa perla (L.) I. Die Entwicklung des Ektoderms in mesodermdefekten Keimteilen. W Roux`s Arch EntwMech Org 141:159–279 Google Scholar Braband A, Richter S, Hiesel R, Scholtz G (2002) Phylogenetic relationships within the Phyllopoda (Crustacea, Branchiopoda) based on mitochondrial and nuclear markers. Mol Phylogenet Evol 25:229–244PubMed CAS Google Scholar Brauer A (1895) Beiträge zur Kenntnis der Entwicklungsgeschichte des Skorpions II. Z Wiss Zool 59:351–435 Google Scholar Bregazzi PK (1973) Embryological development in Tryphosella kergueleni (Miers) and Cheirimedon femoratus (Pfeffer) (Crustacea: Amphipoda). Br Antarct Surv Bull 32:63–74 Google Scholar Brena C, Akam M (2012) The embryonic development of the centipede Strigamia maritima. Dev Biol 363:290–307PubMed CAS Google Scholar Brenneis G, Arango CP, Scholtz G (2011) Morphogenesis of Pseudopallene sp. (Pycnogonida, Callipallenidae) I: Embryonic development. Dev Genes Evol 221:309–328PubMed Google Scholar Campbell LI, Rota-Stabelli O, Edgecombe GD, Marchioro T, Longhorn SJ, Telford MJ, Philippe H, Rebecchi L, Peterson KJ, Pisani D (2011) MicroRNAs and phylogenomics resolve the relationships of Tardigrada and suggest that velvet worms are the sister group of Arthropoda. Proc Natl Acad Sci USA 108:15920–15924PubMed CAS Google Scholar Campos-Ortega JA, Hartenstein V (1985) The Embryonic Development of Drosophila melanogaster. Springer, Berlin Google Scholar Cannon HG (1921) The early development of the summer egg of a cladoceran (Simocephalus vetulus). Quart J Micr Sci 65:627–642 Google Scholar Castellani C, Maas A, Waloszek D, Haug JT (2011) New pentastomids from the late Cambrian of Sweden–deeper insights of the ontogeny of fossil tongue worms. Palaeontographica A 293:95–145 Google Scholar Chen J, Braun A, Waloszek D, Peng Q, Maas A (2004) Lower Cambrian yolk-pyramid embryos from southern Shaanxi, China. Progr Nat Sci 14:167–172 Google Scholar Chipman AD (2008) Thoughts and speculations on the ancestral arthropod segmentation pathway. In: Minelli A, Fusco G (eds) Evolving Pathways. Cambridge University Press, Cambridge, pp 343–358 Google Scholar Chipman AD, Arthur W, Akam M (2004) Early development and segment formation in the centipede, Strigamia maritima (Geophilomorpha). Evol Dev 6:78–89PubMed Google Scholar Claypole AM (1898) The embryology and oogenesis of Anurida maritima. J Morphol 14:219–300 Google Scholar Copf T, Schröder R, Averof M (2004) Ancestral role of caudal genes in axis elongation and segmentation. Proc Natl Acad Sci USA 101:17711–17715PubMed CAS Google Scholar Damen WGM (2002) Parasegmental organization of spider embryos implies that the parasegment is an evolutionary conserved entity in arthropod embryogenesis. Development 129:1239–1250PubMed CAS Google Scholar Davis GK, Patel NH (2002) Short, long, and beyond: molecular and embryological approaches to insect segmentation. Annu Rev Entomol 47:669–699PubMed CAS Google Scholar Dawydoff C (1928) Traité d'embryologie comparée des Invertébrés. Masson, Paris Google Scholar Dearden PK, Donly C, Grbic M (2002) Expression of pair-rule gene homologues in a chelicerate: early patterning of the two-spotted spider mite Tetranychus urticae. Development 129:5461–5472PubMed CAS Google Scholar Delsman HC (1917) Die Embryonalentwicklung von Balanus balanoides Linn. Tijdschr Ned Dierk Ver 2nd series 15:419–520 Google Scholar DiNardo S, Kuner JM, Theis J, O'Farell PH (1985) Development of embryonic pattern in D. melanogaster as revealed by accumulation of the nuclear engrailed protein. Cell 43:59–69PubMed CAS Google Scholar Dogiel V (1913) Embryologische Studien an Pantopoden. Z wiss Zool 107:575–741 Google Scholar Dohle W (1964) Die Embryonalentwicklung von Glomeris marginata (Villers) im Vergleich zur Entwicklung anderer Diplopoden. Zool Jb Anat 81:241–310 Google Scholar Dohle W (1970) Die Bildung und Differenzierung des postnauplialen Keimstreifs von Diastylis rathkei (Crustacea, Cumacea) I. Die Bildung der Teloblasten und ihrer Derivate. Z Morph Ökol Tiere 67:307–392 Google Scholar Dohle W (1972) Über die Bildung und Differenzierung des postnauplialen Keimstreifs von Leptochelia spec. (Crustacea, Tanaidacea). Zool Jb Anat 89:503–566 Google Scholar Dohle W (1979) Vergleichende Entwicklungsgeschichte des Mesoderms bei Articulaten. Fortschr zool Syst Evolutionsf 1:120–140 Google Scholar Dohle W, Gerberding M, Hejnol A, Scholtz G (2004) Cell lineage, segment differentiation, and gene expression in crustaceans. In: Scholtz G (ed) Evolutionary Developmental Biology of Crustacea (Crustacean Issues 15). Balkema, Lisse, pp 95–133 Google Scholar Dohle W, Scholtz G (1988) Clonal analysis of the crustacean segment: the discordance between genealogical and segmental borders. Development 104 Suppl.:147–160 Google Scholar Donoghue PCJ, Bengtson S, Dong X-P, Gostling NJ, Huldtgren T, Cunningham JA, Yin C, Yue Z, Peng F, Stampanoni M (2006) Synchrotron X-ray tomographic microscopy of fossil embryos. Nature 442:680–683PubMed CAS Google Scholar Edgecombe GD (2010) Arthropod phylogeny: an overview from the perspectives of morphology, molecular data and the fossil record. Arthropod Struct Dev 39:74–87PubMed Google Scholar Edgecombe GD, Giribet G (2004) Adding mitochondrial sequence data (16S rRNA and cytochrome c oxidae subunit I) to the phylogeny of centipedes (Myriapoda: Chilopoda): an analysis of morphology and four molecular loci. J Zool Syst Evol Res 42:89–134 Google Scholar Edgecombe GD, Giribet G, Dunn CW, Hejnol A, Kristensen RM, Neves RC, Rouse GW, Worsaae K, Sørensen MV (2011) Higher-level metazoan relationships: recent progress and remaining questions. Org Divers Evol 11:151–172 Google Scholar Eriksson BJ, Tait NN (2012) Early development in the velvet worm Euperipatoides kanangrensis Reid 1996 (Onychophora: Peripatopsidae). Arthropod Struct Dev 41:483–493PubMed Google Scholar Fioroni P (1970) Am Dotteraufschluß beteiligte Organe und Zelltypen bei höheren Krebsen; der Versuch einer einheitlichen Terminologie. Zool Jb Anat 87:481–522 Google Scholar Fioroni P (1987) Allgemeine und vergleichende Embryologie der Tiere. Springer, Berlin Google Scholar Fischer A, Pabst T, Scholtz G (2010) Germ band differentiation in the stomatopod Gonodactylaceus falcatus and the origin of the stereotyped cell division pattern in Malacostraca (Crustacea). Arthropod Struct Dev 39:411–422PubMed Google Scholar Fleig R (1990) Engrailed expression and body segmentation in the honeybee Apis mellifera. Roux`s ArchDev Biol 198:467–473 Google Scholar Frasch M (1999) Intersecting signaling and transcriptional pathways in Drosophila heart specification. Semin Cell Dev Biol 10:61–71PubMed CAS Google Scholar Fuchs K (1914) Die Keimblätterentwicklung von Cyclops viridis Jurine. Zool Jb Anat 38:104–156 Google Scholar Gabriel WN, McNuff R, Patel SK, Gregory TR, Jeck WR, Jones CD, Goldstein B (2007) The tardigrade Hypsibius dujardini, a new model for studying the evolution of development. Dev Biol 312:545–559PubMed CAS Google Scholar George RY, Strömberg J-O (1985) Development of eggs of Antarctic krill Euphausia superba in relation to pressure. Pol Biol 4:125–133 Google Scholar Gerberding M (1994) Superfizielle Furchung, Bildung des Keimstreifs und Differenzierung von Neuroblasten bei Leptodora kindti Focke 1844 (Cladocera, Crustacea). Diplom thesis, Freie Universität Berlin Google Scholar Gerberding M, Browne WE, Patel NH (2002) Cell lineage analysis of the amphipod crustacean Parhyale hawaiensis reveals an early restriction of cell fates. Development 129:5789–5801PubMed CAS Google Scholar Gilbert SF, Raunio AM (eds) (1997) Embryology: constructing the organism. Sinauer Associates, Sunderland Google Scholar Giribet G, Edgecombe GD, Carpenter JM, D'Haese CA, Wheeler WC (2004) Is Ellipura monophyletic? A combined analysis of basal hexapod relationships with emphasis on the origin of insects. Org Divers Evol 4:319–340 Google Scholar Giribet G, Edgecombe GD, Wheeler WC (2001) Arthropod phylogeny based on eight molecular loci and morphology. Nature 413:157–161PubMed CAS Google Scholar Gorham FP (1895) The cleavage of the egg of Virbius zostericola, Smith—a contribution to crustacean cytogeny. J Morph 11:741–746 Google Scholar Grbic M (2003) Polyembryony in parasitic wasps: evolution of a novel mode of development. Int J Dev Biol 47:633–642PubMed Google Scholar Haget A (1953) Analyse expérimentale des facteurs de la morphogenèse embryonnaire chez le coléoptère Leptinotarsa. Bull Biol Fr Belg 87:123–217 Google Scholar Hannibal RL, Price AL, Patel NH (2012) The functional relationship between ectodermal and mesodermal segmentation in the crustacean, Parhyale hawaiensis. Dev Biol 361:427–438PubMed CAS Google Scholar Heider K (1889) Die Embryonalentwicklung von Hydrophilus piceus L. Fischer, Jena Google Scholar Hejnol A, Schnabel R (2005) The eutardigrade Thulinia stephaniae has an indeterminate development and the potential to regulate early blastomere ablations. Development 132:1349–1361PubMed CAS Google Scholar Hertzel G (1985) Die Embryonalentwicklung von Lithobius forficatus (L.) im Vergleich zur Entwicklung anderer Chilopoden. Dissertation, Pädagogische Hochschule Erfurt-Mühlhausen Google Scholar Hertzler PL, Clark WH (1992) Cleavage and gastrulation in the shrimp Sicyonia ingentis: invagination is accompanied by oriented cell division. Development 116:127–140PubMed CAS Google Scholar Heymons R (1901) Die Entwicklungsgeschichte der Scolopender. Zoologica 33:1–244 Google Scholar Hickman VV (1937) The embryology of the syncarid crustacean Anaspides tasmaniae. Pap Proc Roy Soc Tasmania 1936:1–35 Google Scholar Hughes CL, Kaufman TC (2002a) Hox genes and the evolution of the arthropod body plan. Evol Dev 4:459–499PubMed CAS Google Scholar Hughes CL, Kaufman TC (2002b) Exploring the myriapod body plan: expression patterns of the ten Hox genes in a centipede. Development 129:1225–1238PubMed CAS Google Scholar Hughes CL, Kaufman TC (2002c) Exploring myriapod segmentation: the expression patterns of even-skipped, engrailed, and wingless in a centipede. Dev Biol 247:47–61PubMed CAS Google Scholar Ivanov PP (1933) Die embryonale Entwicklung von Limulus moluccanus. Zool Jb Anat 56:163–348 Google Scholar Jacobs DK, Hughes NC, Fitz-Gibbon ST, Winchella CJ (2005) Terminal addition, the Cambrian radiation and the Phanerozoic evolution of bilaterian form. Evol Dev 7:498–514PubMed Google Scholar Janssen R (2012) Segment polarity gene expression in a myriapod reveals conserved and diverged aspects of early head patterning in arthropods. Dev Genes Evol 222:299–309PubMed Google Scholar Janssen R, Prpic N-M, Damen WGM (2006) A review of the correlation of tergites, sternites, and leg pairs in diplopods. Front Zool 2:3; doi:10.1186/1742-9994-3-2 Jenner RA (2010) Higher-level crustacean phylogeny: consensus and conflicting hypotheses. Arthropod Struct Dev 39:143–153PubMed Google Scholar Jura Cz (1965) Embryonic development of Tetrodontophora bielanensis (Waga) (Collembola) from oviposition till germ band formation stage. Acta Biol Cracov Ser Zool 8:141–157 Google Scholar Jura Cz, Krzystofowicz A, Kisiel E (1987) Embryonic development of Tetrodontophora bielanensis (Collembola): Descriptive with scanning electron micrographs. In: Ando H, Jura CZ (eds) Recent Advances in Insect Embryology in Japan and Poland. Arthropod Embryolog Soc Japan, Tsukuba, pp 77–124 Google Scholar Kaudewitz F (1950) Zur Entwicklungsphysiologie von Daphnia pulex. Roux' Arch Entwickl Mech 144:410–447CAS Google Scholar Kanayama M, Akiyama-Oda Y, Oda H (2010) Early embryonic development in the spider Achaearanea tepidariorum: Microinjection verifies that cellularization is complete before the blastoderm stage. Arthropod Struct Dev 39:436–445PubMed Google Scholar Keller R (2006) Mechanisms of elongation in embryogenesis. Development 133:2291–2302PubMed CAS Google Scholar Kimble M, Coursey Y, Ahmad N, Hinsch GW (2002) Behavior of the yolk nuclei during embryogenesis, and development of the midgut diverticulum in the horseshoe crab Limulus polyphemus. Invert Biol 12:365–377 Google Scholar Kingsley JS (1892) The embryology of Limulus. J Morph 7:35–66 Google Scholar Knoll HJ (1974) Untersuchungen zur Entwicklungsgeschichte von Scutigera coleoptrata L. (Chilopoda). Zool Jb Anat 92:47–132 Google Scholar Kohler H-J (1976) Embryologische Untersuchungen an Copepoden: die Entwicklung von Lernaeocera branchialis L. 1767 (Crustacea, Copepoda, Lernaeoida, Lernaeidae). Zool Jb Anat 95:448–504 Google Scholar Kozloff EN (2007) Stages of development, from first cleavage to hatching, of an Echinoderes (Phylum Kinorhyncha: Class Cyclorhagida). Cah Biol Mar 48:199–206 Google Scholar Krause G (1939) Die Eitypen der Insekten. Biol Zentralbl 59:495–536 Google Scholar Kristensen NP (1997) The groundplan and basal diversification of the hexapods. In: Fortey RA, Thomas RH (eds) Arthropod Relationships. Chapman & Hall, London, pp 281–293 Google Scholar Kühn A (1912) Die Sonderung der Keimesbezierke in der Entwicklung der Sommereier von Polyphemus pediculus de Geer. Zool Jb Anat 35:243–340 Google Scholar Laumann M, Bergmann P, Norton RA, Heethoff M (2010a) First cleavages, preblastula and blastula in the parthenogenetic mite Archegozetes longisetosus (Acari, Oribatida) indicate holoblastic rather than superficial cleavage. Arthropod Struct Dev 39:276–286PubMed Google Scholar Laumann M, Norton RA, Heethoff M (2010b) Acarine embryology: inconsistencies, artificial results and misinterpretations. Soil Organ 82:217–235 Google Scholar Lawrence PA (1992) The Making of a Fly. Blackwell, Oxford Google Scholar Lereboullet A (1862) Recherches d'embryologie comparée sur le développement du brochet, de la perche et de l'écrevisse. Mém Acad Sci Inst Fr 17:1–356 Google Scholar Linder F (1952) Contributions to the morphology and taxonomy of the Branchiopoda Notostraca, with special reference to the north American species. Proc U S Nat Mus 102:1–69 Google Scholar Liu PZ, Kaufman TC (2005) Short and long germ segmentation: unanswered questions in the evolution of a developmental mode. Evol Dev 7:629–646PubMed Google Scholar Machida R (2006) Evidence from embryology for reconstructing the relationships of hexapod basal clades. Arthropod Syst Phyl 64:95–104 Google Scholar Machida R, Nagashima T, Ando H (1990) The early embryonic development of the jumping bristletail Pedetontus unimaculatus Machida (Hexapoda: Microcoryphia, Machilidae). J Morph 206:181–195 Google Scholar Malakhov VV, Spiridonov SE (1984) The embryogenesis of Gordius sp. from Turkmenia, with special reference to the position of the Nematomorpha in the animal kingdom. Zool Zh 63:1285–1297 [Russian with English summary] Google Scholar Mallatt JM, Garey JR, Shultz JW (2004) Ecdysozoan phylogeny and Bayesian inference: first use of nearly complete 28S and 18S rRNA gene sequences to classify the arthropods and their kin. Mol Phylogenet Evol 31:178–191PubMed CAS Google Scholar Manton SM (1928) On the embryology of a mysid crustacean Hemimysis lamornae. Phil Trans R Soc B 216:363–463 Google Scholar Manton SM (1934) On the embryology of Nebalia bipes. Phil Trans R Soc B 223:168–238 Google Scholar Manton SM (1949) Studies on the Onychophora VII. The early embryonic stages of Peripatopsis and some general considerations concerning the morphology and phylogeny of the Arthropoda. Phil Trans R Soc B 233:483–580 Google Scholar Manzanares M, Williams TA, Marco R, Garesse R (1996) Segmentation in the crustacean Artemia: engrailed expression studied with an antibody raised against the Artemia protein. Roux`s Arch Dev Biol 205:424–431 Google Scholar Marcus E (1929) Zur Embryologie der Tardigraden. Zool Jb Anat 50:333–384 Google Scholar Martin BL, Kimelman D (2009) Wnt signaling and the evolution of embryonic posterior development. Curr Biol 19:R215–R219PubMed CAS Google Scholar Mayer G, Kato C, Quast B, Chisholm RH, Landman KA, Quinn LM (2010) Growth patterns in Onychophora (velvet worms): lack of a localised posterior proliferation zone. BMC Evol Biol 10:339; doi:10.1186/1471-2148-10-339 McMurrich JP (1895) Embryology of the isopod Crustacea. J Morph 11:63–154 Google Scholar Meschenmoser M (1996) Dorsal- und Lateralorgane in der Embryonalentwicklung von Peracariden (Crustacea, Malacostraca). Cuvillier Verlag, Göttingen Google Scholar Meusemann K, von Reumont BM, Simon S, Roeding F, Strauss S, Kück P, Ebersberger I, Walzl M, Pass G, Breuers S, Achter V, von Haeseler A, Burmester T, Hadrys H, Wägele JW, Misof B (2010) A phylogenomic approach to resolve the arthropod tree of life. Mol Biol Evol 27:2451–2464PubMed CAS Google Scholar Minelli A (2001) A three-phase model of arthropod segmentation. Dev Genes Evol 211:509–521PubMed CAS Google Scholar Minelli A (2005) A morphologist's perspective on terminal growth and segmentation. Evol Dev 7:568–573PubMed Google Scholar Mittmann B, Wolff C (2012) Embryonic development and staging of the cobweb spider Parasteatoda tepidariorum C. L. Koch, 1841 (syn.: Achaearanea tepidariorum; Araneomorphae; Theridiidae). Dev Genes Evol 222:189–216PubMed Google Scholar Møller OS, Olesen J, Avenant-Oldewage A, Thompson PF, Glenner H (2008) First maxillae suction discs in Branchiura (Crustacea): development and evolution in light of the first molecular phylogeny of Branchiura, Pentastomida, and other "Maxillopoda". Arthropod Struct Dev 37:333–346PubMed Google Scholar Montuy-Gómez D, Gómez-Gutiérrez J, Rodríguez-Jaramillo C, Robinson CJ (2012) Nyctiphanes simplex (Crustacea: Euphausiacea) temporal association of embryogenesis and early larval development with female molt and ovarian cycles. J Plankt Res 34:531–547 Google Scholar Morgan TH (1891) A contribution to the embryology and phylogeny of the Pycnogonida. Stud Biol Lab J Hopkins Univ 5:1–76 Google Scholar Moritz M (1957) Zur Embryonalentwicklung der Phalangiiden (Opiliones, Palpatores) unter besonderer Berücksichtigung der äußeren Morphologie, der Bildung des Mitteldarmes und der Genitalanlage. Zool Jb Anat 76:331–370 Google Scholar Moritz M (1993) Unterstamm Arachnata. In: Gruner H-E (ed) Lehrbuch der speziellen Zoologie, Band I, 4.Teil Arthropoda. Gustav Fischer, Jena, pp. 64–442 Google Scholar Müller YMR (1984) Die Embryonalentwicklung von Macrobrachium carcinus (L.) (Malacostraca, Decapoda, Natantia). Zool Jb Anat 112:51–78 Google Scholar Müller-Calé K (1913) Die Entwicklung von Cypris incongruens. Zool Jb Anat 36:113–170 Google Scholar Nielsen C (2001) Animal Evolution: Interrelationships of the Living Phyla, 2nd edn. Oxford University Press, Oxford Google Scholar Nielsen C (2012) Animal Evolution: Interrelationships of the Living Phyla, 3rd edn. Oxford University Press, Oxford Google Scholar Olesen J (2009) Phylogeny of Branchiopoda (Crustacea): character evolution and contribution of uniquely preserved fossils. Arthr Syst Phyl 67:3–39 Google Scholar Osche G (1963) Die systematische Stellung und Phylogenie der Pentastomida–embryologische und vergleichend-anatomische Studien an Reighardia sternae. Z Morph Ökol Tiere 52:487–596 Google Scholar Patel NH, Condron BG, Zinn K (1994) Pair-rule expression patterns of even-skipped are found in both short- and long-germ beetles. Nature 367:429–434PubMed CAS Google Scholar Patel NH, Kornberg TB, Goodman CS (1989) Expression of engrailed during segmentation of grasshopper and crayfish. Development 107:201–212PubMed CAS Google Scholar Paulus H (2007) Arthropoda. In: Westheide W, Rieger R (eds) Spezielle Zoologie, Teil 1: Einzeller und wirbellose Tiere. Spektrum, München, pp 438–446 Google Scholar Peel AD, Chipman AD, Akam M (2005) Arthropod segmentation: beyond the Drosophila paradigm. Nature Rev Gen 6:905–916CAS Google Scholar Peterson KJ, Eernisse DJ (2001) Animal phylogeny and the ancestry of bilaterians: inferences from morphological and 18S rDNA sequences. Evol Dev 3:170–205PubMed CAS Google Scholar Pflugfelder O (1962) Lehrbuch der Entwicklungsgeschichte und Entwicklungsphysiologie der Tiere. VEB Gustav Fischer, Jena Google Scholar Pisani D, Poling LL, Lyons-Weiler M, Hedges SB (2004) The colonization of land by animals: molecular phylogeny and divergence times among arthropods. BMC Biol 2:1; doi:10.1186/1741-7007-2-1 Price AL, Modrell MS, Hannibal RL, Patel NH (2010) Mesoderm and ectoderm lineages in the crustacean Parhyale hawaiensis display intra-germ layer compensation. Dev Biol 341:256–266PubMed CAS Google Scholar Rathke H (1829) Untersuchungen über Bildung und Entwicklung des Flusskrebses. Leopold Voss, Leipzig Google Scholar Regier JC, Shultz JW, Zwick A, Hussey A, Ball B, Wetzer R, Martin JW, Cunningham CW (2010) Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. Nature 463:1079–1083PubMed CAS Google Scholar Reichenbach H (1886) Studien zur Entwicklungsgeschichte des Flusskrebses. Abhandl Senckenb Naturforsch Gesellsch 14:1–137 Google Scholar Reid AL (1996) Review of the Peripatopsidae (Onychophora) in Australia, with comments on peripatopsid relationships. Invert Tax 10:663–936 Google Scholar Richter S, Olesen J, Wheeler WC (2007) Phylogeny of Branchiopoda (Crustacea) based on a combined analysis of morphological data and six molecular loci. Cladistics 23:301–336 Google Scholar Richter S, Scholtz G (2001) Phylogenetic analysis of the Malacostraca (Crustacea). J Zool Syst Evol Res 39:113–136 Google Scholar Samter M (1900) Studien zur Entwicklungsgeschichte der Leptodora hyalina Lillj. Z wiss Zool 63:169–260 Google Scholar Sanchez S (1959) Le développement des Pycnogonides et leurs affinités avec les Arachnides. Arch Zool Exp Gén 98:1–102 Google Scholar Sander K (1983) The Evolution of patterning mechanisms: gleanings from insect embryogenesis and spermatogenesis. In: Goodwin BC, Holder N, Wylie CG (eds) Development and Evolution. Cambridge University Press, Cambridge, pp 137–158 Google Scholar Sanders KL, Lee MS (2010) Arthropod molecular divergence times and the Cambrian origin of pentastomids. Syst Biodiv 8:63–74 Google Scholar Scheidegger G (1976) Stadien der Embryonalentwicklung von Eupagurus prideauxi Leach (Crustacea, Decapoda Anomura), unter besonderer Berücksichtigung der Darmentwicklung und der am Dotterabbau beteiligten Zelltypen. Zool Jb Anat 95:297–353 Google Scholar Schimkewitsch L, Schimkewitsch W (1911) Ein Beitrag zur Entwicklungsgeschichte der Tetrapneumones, Teil I. Bull Acad Imp Sci St Petersb 6th series 5:637–654 Google Scholar Schimkewitsch W (1896) Studien über parasitische Copepoden. Z wiss Zool 61:339–362 Google Scholar Schimkewitsch W (1903) Über die Entwicklung von Telyphonus caudatus (L.). Zool Anz 26:665–685 Google Scholar Scholl G (1963) Embryologische Untersuchungen an Tanaidaceen (Heterotanais oerstedi Kröyer). Zool Jb Anat 80:500–554 Google Scholar Scholtz G (1984) Untersuchungen zur Bildung und Differenzierung des postnauplialen Keimstreifs von Neomysis integer Leach (Crustacea, Malacostraca, Peracarida). Zool Jb Anat 112:295–349 Google Scholar Scholtz G (1990) The formation, differentiation and segmentation of the post-naupliar germ band of the amphipod Gammarus pulex L. (Crustacea, Malacostraca, Peracarida). Proc R Soc Lond B 239:163-211 Google Scholar Scholtz G (1992) Cell lineage studies in the crayfish Cherax destructor (Crustacea, Decapoda): germ band formation, segmentation, and early neurogenesis. Roux`s Arch Dev Biol 202:36–48 Google Scholar Scholtz G (1997) Cleavage, germ band formation and head segmentation: the ground pattern of the Euarthropoda. In: Fortey RA, Thomas RH (eds) Arthropod Relationships. Chapman & Hall, London, pp 317–332 Google Scholar Scholtz G (2002) The Articulata hypothesis—or what is a segment? Org Divers Evol 2:197–215 Google Scholar Scholtz G (2005) Homology and ontogeny: pattern and process in comparative developmental biology. Theory Biosci 124:121–143PubMed Google Scholar Scholtz G, Abzhanov A, Alwes F, Biffis C, Pint J (2009a) Development, genes, and decapod evolution. In: Martin JW, Crandall KA, Felder DL (eds) Decapod Crustacean Phylogenetics (Crustacean Issues 18). CRC Press & Taylor and Francis, Boca Raton, pp 31–46 Google Scholar Scholtz G, Dohle W (1996) Cell lineage and cell fate in crustacean embryos—a comparative approach. Int J Dev Biol 40:211–220PubMed CAS Google Scholar Scholtz G, Patel NH, Dohle W (1994) Serially homologous engrailed stripes are generated via different cell lineages in the germ band of amphipod crustaceans (Malacostraca, Peracarida). Int J Dev Biol 38:471–478PubMed CAS Google Scholar Scholtz G, Ponomarenko E, Wolff C (2009b) Cirripede cleavage patterns and the origin of the Rhizocephala (Crustacea: Thecostraca). Arthropod Syst Phyl 67:219–228 Google Scholar Scholtz G, Wolff C (2002) Cleavage pattern, gastrulation, and germ disc formation of the amphipod crustacean Orchestia cavimana. Contrib Zool 71:9–28 Google Scholar Schulze J, Schierenberg E (2011) Evolution of embryonic development in nematodes. EvoDevo 2:18. doi:10.1186/2041-9139-2-18 Schwartz V (1973) Vergleichende Entwicklungsgeschichte der Tiere. Georg Thieme, Stuttgart Google Scholar Seaver EC, Thamm K, Hill SD (2005) Growth patterns during segmentation in two polychaete annelids, Capitella sp. I and Hydroides elegans: comparisons at distinct life history stages. Evol Dev 7:312–326PubMed Google Scholar Seitz K-A (1966) Normale Entwicklung des Arachniden-Embryos Cupiennius salei (Keyserling) und seine Regulationsfähigkeit nach Röntgenbestrahlungen. Zool Jb Anat 83:327–447 Google Scholar Shankland M (1999) Anteroposterior pattern formation in the leech embryo. In: Moody SA (ed) Cell lineage and cell fate determination. Academic Press, San Diego, pp 207–224 Google Scholar Shear WA, Edgecombe GD (2010) The geological record and phylogeny of Myriapoda. Arthropod Struct Dev 39:174–190PubMed Google Scholar Sheldon L (1887) On the development of Peripatus novae-zealandiae. Q J Microsc Sci 28:205–237 Google Scholar Shiino SM (1942) Studies on the embryonic development of Squilla oratoria de Haan. Mem Coll Sci Kyoto Univ B 28:77–174 Google Scholar Shimizu T, Nakamoto A (2001) Segmentation in annelids: cellular and molecular basis for metameric body plan. Zool Sci 18:285–298 Google Scholar Shultz JW (2007) A phylogenetic analysis of the arachnid orders based on morphological characters. Zool J Linn Soc 150:221–265 Google Scholar Siewing R (1979) Homology of cleavage-types? Fortschr zool Syst Evolutionsf 1:7–18 Google Scholar Sograff N (1883) Materials toward the knowledge of the embryonic development of Geophilus ferrugineus and Geophilus proximus. Izveˆstya Imperatorskago Obshchestva Lyubitelei Estestvoznaniya, Antropologii i Etnografii pri Imperatorskom Moskovskom Universitete 2:1–77 (in Russian) Google Scholar Strömberg JO (1971) Contribution to the embryology of bopyrid isopods with special reference to Bopyrides, Hemiarthrus and Pseudione (Isopoda, Epicaridea). Sarsia 47:1–46 Google Scholar Tardent P (1978) Coelenterata, Cnidaria. In: Seidel F (ed) Morphogenese der Tiere, Erste Reihe: Deskriptive Morphogenese, Lieferung I: A-I. VEB Gustav Fischer, Jena Google Scholar Taube E (1909) Beiträge zur Entwicklungsgeschichte der Euphausiiden. I. Die Furchung des Eies bis zur Gastrulation. Z wiss Zool 92:427–464 Google Scholar Tiegs OW (1940) The embryology and affinities of the Symphyla, based on a study of Hanseniella agilis. Q J Microsc Sci 82:1–225 Google Scholar Tiegs OW (1947) The development and affinities of the Pauropoda, based on a study of Pauropus silvaticus. Q J Microsc Sci 88:275–336 Google Scholar Tojo K, Machida R (1998) Early embryonic development of the mayfly Ephemera japonica McLachlan (Insecta: Ephemeroptera, Ephemeridae). J Morph 238:327–335 Google Scholar Turquier Y (1967) L'embryogenése de Trypetesa nassarioides Turquier (Cirripède Acrothoracique). Ses rapports avec celle des autres Cirripèdes. Arch Zool Exp Gén 108:111–137 Google Scholar Ungerer P, Scholtz G (2009) Cleavage and gastrulation in Pycnogonum litorale (Arthropoda, Pycnogonida): morphological support for the Ecdysozoa? Zoomorphology 128:263–274 Google Scholar Vollmer C (1912) Zur Entwicklung der Cladoceren aus dem Dauerei. Z wiss Zool 102:646–700 Google Scholar von Baldass F (1941) Entwicklung von Daphnia pulex. Zool Jb Anat 67:1–60 Google Scholar von Reumont BM, Jenner RA, Wills MA, Dell'Ampio E, Pass G, Ebersberger I, Meyer B, Koenemann S, Iliffe TM, Stamatakis A, Niehuis O, Meusemann K, Misof B (2012) Pancrustacean phylogeny in the light of new phylogenomic data: Support for Remipedia as the possible sister group of Hexapoda. Mol Biol Evol 29:1031–1045 Google Scholar von Wistinghausen C (1891) Untersuchungen über die Entwicklung von Nereis dumerilii. Mitt Zool Stat Neapel 10:41–74 Google Scholar Waloszek D, Maas A (2005) The evolutionary history of crustacean segmentation: a fossil-based perspective. Evol Dev 7:515–527PubMed Google Scholar Weldon WFR (1892) The formation of the germ-layers in Crangon vulgaris. Q J Microsc Sci 33:343–363 Google Scholar Wennberg SA, Janssen R, Budd GE (2008) Early embryonic development of the priapulid worm Priapulus caudatus. Evol Dev 10:326–338PubMed Google Scholar Weygoldt P (1960a) Mehrphasige Gastrulation bei Arthropoden. Zool Anz 164:381–395 Google Scholar Weygoldt P (1960b) Embryonaluntersuchungen an Ostracoden. Die Entwicklung von Cyprideis litoralis. Zool Jb Anat 78:369–426 Google Scholar Weygoldt P (1963) Grundorganisation und Primitiventwicklung bei Articulaten. Zool Anz 171:363–376 Google Scholar Weygoldt P (1964) Vergleichend-embryologische Untersuchungen an Pseudoskorpionen (Chelonethi). Z Morph Ökol Tiere 54:1–106 Google Scholar Weygoldt P (1975) Untersuchungen zur Embryologie und Morphologie der Geißelspinne Tarantula marginemaculata C. L. Koch (Arachnida, Amblypygi, Tarantulidae). Zoomorphologie 82:137–199 Google Scholar Weygoldt P (1979) Gastrulation in arthropods? Fortschr zool Syst Evolutionsf 1:73–81 Google Scholar Weygoldt P (1986) Arthropod interrelationships–the phylogenetic-systematic approach. Z Zool Syst Evolut-forsch 24:19–35 Google Scholar Weygoldt P, Paulus HF (1979) Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. II. Cladogramme und die Entfaltung der Chelicerata. Morphologische Untersuchungen. Z zool Syst Evolut-forsch 17:117–200 Google Scholar Williams T, Blachuta B, Hegna TA, Nagy LM (2012) Decoupling elongation and segmentation: Notch involvement in anostracan crustacean segmentation. Evol Dev 14:372–382PubMed CAS Google Scholar Wolff C (2009) The embryonic development of the malacostracan crustacean Porcellio scaber (Isopoda, Oniscidea). Dev Genes Evol 219:545–564PubMed Google Scholar Wolff C, Hilbrant M (2011) The embryonic development of the Central American wandering spider Cupiennius salei. Front Zool 8:15. doi:10.1186/1742-9994-8-15 Wolff C, Scholtz G (2002) Cell lineage, axis formation, and the origin of germ layers in the amphipod crustacean Orchestia cavimana. Dev Biol 250:44–58PubMed CAS Google Scholar Zantke J, Wolff C, Scholtz G (2008) Three-dimensional reconstruction of the central nervous system of Macrobiotus hufelandi (Eutardigrada, Parachela): implications for the phylogenetic position of Tardigrada. Zoomorphology 127:21–36 Google Scholar Zehnder H (1934) Über die Embryonalentwicklung des Flusskrebses. Acta Zool 15:261–408 Google Scholar Zilch R (1974) Die Embryonalentwicklung von Thermosbaena mirabilis Monod (Crustacea, Malacostraca, Pancarida). Zool Jb Anat 93:462–576 Google Scholar Zilch R (1979) Cell lineage in arthropods? Fortschr zool Syst Evolutionsforsch 1:19–41 Google Scholar Zrzavý J, Hypša V, Vlášková M (1998) Arthropod phylogeny: taxonomic congruence, total evidence and conditional combination approaches to morphological and molecular data sets. In: Fortey RA, Thomas RH (eds) Arthropod Relationships. Chapman & Hall, London, pp 97–107 Google Scholar

2019 Oct 2;286(1912):20191881. doi: 10.1098/rspb.2019.1881

Segmentation is fundamental to the arthropod body plan. Understanding the evolutionary steps by which arthropods became segmented is being transformed by the integration of data from evolutionary developmental biology (evo-devo), Cambrian fossils that allow the stepwise acquisition of segmental characters to be traced in the arthropod stem-group, and the incorporation of fossils into an increasingly well-supported phylogenetic framework for extant arthropods based on genomic-scale datasets. Both evo-devo and palaeontology make novel predictions about the evolution of segmentation that serve as testable hypotheses for the other, complementary data source. Fossils underpin such hypotheses as arthropodization originating in a frontal appendage and then being co-opted into other segments, and segmentation of the endodermal midgut in the arthropod stem-group. Insights from development, such as tagmatization being associated with different modes of segment generation in different body regions, and a distinct patterning of the anterior head segments, are complemented by palaeontological evidence for the pattern of tagmatization during ontogeny of exceptionally preserved fossils. Fossil and developmental data together provide evidence for a short head in stem-group arthropods and the mechanism of its formation and retention. Future breakthroughs are expected from identification of molecular signatures of developmental innovations within a phylogenetic framework, and from a focus on later developmental stages to identify the differentiation of repeated units of different systems within segmental precursors.

Keywords: evo-devo, Arthropoda, palaeontology

Questions about deep evolutionary history, such as the origin and evolution of animal body plans, demand a combined approach that takes into account multiple sources of evidence. These historical questions are often extremely complex, and are shrouded in the mists of deep time, so that no single approach provides enough information to fully reconstruct the underlying evolutionary events. At the very least, understanding deep evolution requires a sound phylogenetic framework, an adequate fossil record, and a mechanistic/developmental view of morphology [1]. Phylogenetics provides the framework within which we can infer the history of specific characters—how many times a feature evolved and on which branches of the tree of life. Palaeontology calibrates an evolutionary timescale, a putative sequence of events, and direct evidence of extinct morphologies and unique combinations of characters. Development provides insights into the processes by which form is generated, and about the possible transformation series between morphologies. How segmented body plans originated in arthropods exemplifies a question about deep evolutionary history, one for which progress has been informed by these diverse perspectives. Arthropods are by far the most successful animal phylum and their success is largely an outcome of their segmented body. A segmentally arranged body allows for different measures of autonomy of individual segments or batches of segments, which is manifest in the varied tagmatization of the arthropod body and the 'Swiss Army knife'-like specialization of appendages to perform diverse functions. This modularity in specialization has allowed arthropods to evolve and adapt to numerous environments and to specialize to myriad locomotory and feeding strategies. The success of arthropods is not confined to the present. Indeed, arthropods have probably been the most common and diverse animals throughout their evolutionary history [2], and fossils show that the segmented body plan evolved very early in arthropod evolution. A segmented body is found in three phyla: Arthropoda, Chordata and Annelida, and evolved convergently in the three cases [3]. The segmental organization of the body in all three cases probably evolved in a stepwise fashion from an unsegmented ancestor, via recruitment of different metameric organ systems into synchronized repeated body units and the co-option of the development of these organ systems into unified embryonic segments [4]. Beyond this hypothetical scenario (figure 1), we have only patchy data about the evolutionary processes that led to the appearance of the segmented body in arthropods, or about the intermediate stages in this presumed stepwise process. Nonetheless, we can learn about the evolution of the segmented body by understanding the evolution of the developmental process that underlies it—the segmentation process. A scenario for the origin and evolution of arthropod segmentation (based on [4]). (a) A simple bilaterian with a short body; (b) extension of the anterior–posterior axis (A-P); (c) several organ systems become independently metameric and distributed along the A-P axis; (d) metamerism of the different systems becomes synchronized; (e) elements of all metameric systems are generated together from an undifferentiated segmental precursor. (Online version in colour.) Evolutionary developmental biology (evo-devo) is the discipline that focuses on tracing changes in developmental processes over time, through a tree-based comparison of development in different organisms. This approach allows us to pinpoint where in phylogeny specific developmental characters first evolved or where they were modified. This provides insight into the evolution of morphological characters that are under selection, and about the mechanisms behind the generation of the characters and how they can be modified through changes in the developmental process. By contrast, the fossil record provides information about the temporal context of morphological changes; minimum dates for when specific morphologies appeared and in what sequence; while also providing examples of specific character combinations and intermediate character states that are not found in extant species. There is a complementarity between one approach that looks at a single moment in time (the present), but allows mechanistic analyses of developmental processes, and an approach that gives a much deeper temporal perspective but is limited by the unpredictable preservation of a sample of body plans, and of course does not allow experimentation. Integration of evo-devo approaches and fossil data has been a productive approach in the vertebrate world for years [5–7]. Many of the fundamentals of evo-devo have, however, been established using arthropods [8–14], and this early work was instrumental in consolidating the evo-devo approach as an independent evolutionary discipline. There has been some effort to integrate evo-devo and palaeontological perspectives on the origin of various arthropod features (e.g. insect wings [15,16], head segmentation [17], appendages [18] and trunk segmentation [19]), but this approach remains under-used in the world of arthropod evolutionary biology. With respect to the specific question we are addressing here—the origin of segmental features—palaeontological effort is concentrated in the Cambrian, that being the time period when arthropods first appear in the fossil record and when stem-group arthropods are best represented. The quality of early arthropod fossils and their interpretation have steadily improved via the documentation of Cambrian fossils from sites of exceptional preservation [2], which continue to be discovered [20]. These fossils underpin current hypotheses about how a grade of taxa that constitutes the arthropod stem-group reveals the stepwise acquisition of characters, many related to segmentation. Burgess Shale-type fossils—two-dimensional carbonaceous compressions of the cuticle coupled with mineralization of labile tissue such as the gut and muscle—have been the focus of much research, but have been supplemented by finds from other styles of fossilization (e.g. small carbonaceous fossils [21] and secondarily phosphatized 'Orsten' fossils, including larvae [22]). The latter are especially important for preserving series of developmental stages that bridge gaps between embryos (which underpin much evo-devo research) and adult stages, which predominate among Burgess Shale-type fossils [23,24]. In parallel, the representation of species and taxa in the experimental world has increased substantially. This broader selection of species covers a much wider and more representative sample of extant morphological diversity within arthropods than that represented by the very small sample of model species available until only 15 years ago (e.g. hemimetabolous insects [25,26]; diverse arachnids [27–30] and dipterans [31–34]; non-hexapod pancrustaceans: [35–37]; myriapods [38,39]; and many others). This broader range of model species has allowed the addressing of specific evolutionary questions, such as the origin of different respiratory organs [30], the origin of wings [40,41] and the diversity of limbs [18]. Beyond the increase in experimentally tractable model organisms, the explosion of available genomes [42] makes it possible to use bioinformatic approaches to look for genetic and regulatory novelties, and makes it easier to plan and develop functional work on an even larger sample of arthropod diversity. With regards to segmentation in particular, emerging model arthropods have shed light on the diversity of segment generation modes and the evolution of the segmentation process in insects and other arthropods [43–49]. The phylogenetic relationships of extant arthropods used as models in evo-devo are resolved with considerable confidence based on genome scale data (figure 2 top, reviewed by Giribet & Edgecombe [50]). High-level insect phylogeny has a well-supported, morphologically coherent framework based on transcriptomic analyses [51], the pattern of 'crustacean' paraphyly with respect to Hexapoda has numerous nodes that are repeatedly recovered with strong support in phylogenomic studies [52,53], and myriapod phylogeny has settled on higher-level clades that reflect groups long recognized based on morphology and development [54,55]. Chelicerate phylogeny remains more ambiguous, but some key nodes bracketing evo-devo models (such as spiders and scorpions being more closely related to each other than either is to mites, i.e. the Arachnopulmonata hypothesis) are robustly supported [56,57]. Phylogenetic relationships among key experimental model species of Panarthropoda and representative fossil taxa. Names of terminals at the top of the tree are extant genera of experimentally tractable model species. Names of terminals deep within the tree are fossil forms representing stem-groups of various extant taxa. Node names refer to crown-groups. Placement of some of the fossil taxa is still contentious (see text for examples).The phylogenetic position of fossils on the other hand is often contentious. Over a decade or so, a picture had emerged of the branching sequence in the arthropod stem-group (figure 2; reviewed by Daley et al. [58]), a grade that encompasses a transition from vermiform, lobopod-bearing forms in the deepest nodes of the arthropod stem-group to fully arthrodized and arthropodized forms more proximal to the crown-group. Because it samples morphologies between the most recent common ancestor of Onychophora (which lack segmental sclerites) and extant diversity of Arthropoda, this grade is of particular relevance to understanding the evolution of arthropod segmentation. Some taxa are consistently recovered in the arthropod stem-group in all recent phylogenetic analyses, such as Isoxys and Radiodonta (the clade including Anomalocaris and its relatives), but a few groups that had been assigned to the arthropod stem-group have been reinterpreted as within the arthropod crown-group. This affects some fossil clades that had played a significant role in resolving character acquisition in the arthropod stem-group, such as fuxianhuiids and bivalved hymenocarine arthropods like Canadaspis and Branchiocaris [59,60]. Different interpretations of morphology, especially with regards to mouthpart differentiation, together with alternative character sets and tree reconstruction methods, have prompted a shift of fuxianhuiids and Hymenocarina into the arthropod crown-group, either within or allied to Mandibulata [61,62]. A combined approach, including both the fossil record and experimental data on extant animals, within a unified phylogenetic framework (figure 2) provides the most complete possible picture of the evolution of the arthropod segmented body. The fossil record contributes data about the sequence of character acquisition, most informatively when characters that are clustered at a single node in extant taxa are scattered across multiple nodes in a stem-group. Furthermore, because fossils preserve unique combinations of characters, some of which may be lost in extant taxa, they can serve as the basis for novel hypotheses on the stepwise assembly of the developmental programme that generates segments in extant taxa. Conversely, development provides mechanistic examples of how characters are transformed, which allow linking character states in fossil taxa and suggest putative homologies that are not obvious from the fossils alone. We provide examples of these reciprocities and synergies in the following. The deepest branches of the arthropod stem-group are represented by large-bodied Cambrian lobopodians such as Jianshanopodia [63], Megadictyon [64] and Siberion [65]. These have annulated trunks with a homonomous series of annulated lobopods. The anteriormost appendage pair is specialized as an enlarged raptorial pair of limbs bearing strong, elongate spines along their inner margins, but like the trunk appendages they too are annulated. An annulated, spinose frontal appendage is shared by the so-called gilled lobopodians—exemplified by the early Cambrian Kerygmachela (figure 3a) and Pambdelurion—that are broadly agreed to branch more crownward of the giant lobopodians in the arthropod stem-group. Traces of neural tissue innervating the frontal appendage of Kerygmachela have been interpreted as nerves derived from the first brain ganglion—the protocerebrum [67]. Annulated (a) and arthropodized (b–e) frontal appendages (fa). (a) The 'gilled lobopodian' Kerygmachela kierkegaardi; (b–e) disarticulated Anomalocaris canadensis frontal appendages. Scales: (a–c) 10 mm, (d–e) 5 mm. (a) courtesy of J. Vinther; (b–e) courtesy of A. Daley (from [66]). (Online version in colour.)The origin of fully arthropodized appendages in the arthropod stem-group can be linked to the group known as Radiodonta, exemplified by the famous Anomalocaris. Radiodonts have an arthropodized frontal appendage, in most members of the group this being the only conspicuously arthropodized appendage in the body. Various theories interpret other segmental body parts, notably a fringe of dorsal setal blades and series of paired ventral flaps, as appendicular derivatives, homologues of the rami of biramous appendages in arthropods [68,69], but the frontal appendage most clearly depicts apomorphies of arthropodization. The radiodont frontal appendage has discrete sclerotized articles/podomeres that are articulated to each other on their dorsal side at hinges and are separated from each other on their ventral sides by desclerotized triangular, telescoping fields of arthrodial membrane [66] (figure 3b–e). Most podomeres bear ventral spines, corresponding to endites in many crown- (and stem-) group arthropods, and a few distal podomeres bear dorsal spines as well. Extant panarthropods present two character states, each corresponding to one of the two states observed in frontal appendages in the arthropod stem-group: fully arthropodized limbs with a more or less conserved array of elements, and the annulated, lobopodial limbs of onychophorans and tardigrades. The network patterning the arthropodized limb is conserved to a very high degree among all arthropods [18,70]. The gap genes that pattern the proximo-distal axis of arthropod limbs are expressed in the same register in onychophorans [71,72], demonstrating that these genes have a conserved role in limb development in panarthropods that predates arthropodization (figure 4). Thus, it is possible to reconstruct the gene regulatory networks (GRNs) that were instrumental in the evolution of panarthropod limbs and in their subsequent arthropodization. Schematic of gap gene expression domains in limbs of onychophorans and in the different arthropod classes. The proximal side of the limb is to the left. Lighter colours represent lower expression levels or downregulation during development. Redrawn with a revised phylogeny from [70]. See source for references. (Online version in colour.)Radiodonts and more crownward taxa in the arthropod stem-group demonstrate that arthropodization did not happen in a piecemeal manner (e.g. one segment at a time posteriorly from an origin in the protocerebral segment). Rather, it was co-opted by the rest of the head and trunk segments simultaneously [18] and, notably, was abandoned in the protocerebral segment (acknowledging a prolonged debate about whether the labrum is or is not appendicular and specifically a transformed protocerebral appendage; reviewed by Ortega-Hernández et al. [17] and Jockusch [18]). Arthropods immediately crownward of radiodonts in the arthropod stem-group, such as isoxyids, display arthropodization of all head and trunk limbs, presumed to be a shared derived character retained by crown-group arthropods. This is the condition in Deuteropoda (sensu [73]), a monophyletic group united by a deutocerebral first appendage (antenna or chelicera), encompassing all crown-group arthropods and a set of stem-group taxa. The detailed similarity in the structure of the arthropodized frontal appendage in radiodonts to the arthropodized trunk limbs in more crownward groups suggests that these are serially homologous structures. Homology implies that they are underlain by the same GRN or character identity network (CHiN, [74]), even though they are found on positionally non-equivalent segments. If this is indeed the case, then the modified limb patterning GRN (which allows arthropodization of the limb) was co-opted from the frontal appendage to other appendages. The concept of co-option is a central tenet in the theory of novelty within the evo-devo conceptual framework [75–78]. According to the accepted paradigm, novel structures can arise through the recruitment of existing GRNs to novel locations. For this to happen, all that is required is for a key gene, high in the GRN's hierarchy, to be activated ectopically, and this will suffice for the activation of the entire network and the generation of a complete structure in a new location, in essence creating an evolutionary novelty. Arthropod tagmata are fundamentally defined by differentiation of segmental structures, such as differential presence or absence of appendages, or differences in the structure of batches of appendages. Evo-devo research has now elucidated many of the mechanisms responsible for the presence or the absence of appendages on specific segments—characteristic for different tagmata. Dll is generally considered to be the main signal for the initiation of the limb development programme [5,79]. The identity of the segments and the identity of the appendages they bear (if any) are mostly under the control of Hox genes, often directly regulating Dll [80], although it is clear that this is only a partial description of the tagma differentiation process. In most cases, Hox gene expression defines broad domains along the anterior–posterior (A-P) axis, but does not define the borders between tagmata [81]. The fossil record predicts that the plesiomorphic state (post-recruitment of arthropodized limbs to the trunk) is a series of more or less homonomous appendages on all post-cephalic segments. However, most arthropod lineages show examples of segment specialization and loss of appendages in some segments. The best-known example is the differentiation of the extant insect body into head, thorax and abdomen, but tagmatization is also well known from extinct groups. Fuxianhuiids, for example, have appendages on the anterior part of the trunk but have a limbless batch of segments in the posterior part of the trunk [82], analogous to the abdomen of extant arthropods (e.g. hexapods). Complex patterns of limb loss and regional differentiation are known in stem- and crown-group chelicerates [83]. Some arthropods display different ontogenetic modes of segment generation in different body regions. In some cases, these differences correlate fully with different tagmata. This is best studied in insects, specifically in the milkweed bug Oncopeltus fasciatus, in which thoracic segments are generated simultaneously, whereas abdominal segments are generated sequentially [48]. While this question has not been addressed specifically in other insects, expression data from the cricket Gryllus bimaculatus [84] suggest this may be a common pattern, at least in hemimetabolous insects. This pattern is not seen in Holometabola, which could indicate a secondary loss of region-specific segmentation modes. In Myriapoda, the head segments are formed separately and not in temporal sequence along the A-P axis, in contrast with the trunk segments, which form in strict A-P sequence [46]. Spiders have a different prosomal and opisthosomal segmentation process [85,86] and in the mite Tetranychus the pair-rule orthologue Pax-3/7 is expressed only in the prosoma [87]. Ontogenetic data for fossil taxa are rare, but there are at least some cases that conform to this pattern. The ontogeny of Fuxianhuia protensa shows that tergites form at a terminal growth zone, and moults involving tergite addition alternate with ones in which a limbless abdominal segment is shed into the appendage-bearing thorax [82]. If fuxianhuiids are stem-group arthropods, as is widely accepted, an association between tagmosis (including presence versus absence of appendages on tagmata) and different modes of segment generation predates the origin of the arthropod crown-group. Thus, we would predict that different modes of segment generation within a single species existed very early in arthropod evolution. The fossil record shows that the ancestral arthropod head was composed of fewer segments than that of extant arthropods. Deeply diverging stem-group euarthropods (lobopodians such as Megadictyon and Jianshanopodia and the gilled lobopodians Kerygmachela and Pambdelurion) had a single-segment head, the protocerebral segment bearing the sole appendage pair, a frontal appendage [17,67] (figure 3a). This situation of a head composed of a single protocerebral segment is still found in tardigrades [88,89]. More crownward of these, Radiodonta for the most part correspond to this level of organization, but the number of head segments in this clade is ambiguous because of whether or not three segments associated with small flaps and in some cases paired gnathobase-like structures [90] are a part of the head or the trunk. Taxa closer to the euarthropod crown-group, such as Fuxianhuia [91], have three head segments, in this case being ocular, an antennule and a so-called 'SPA'—a specialized post-antennal appendage. On this basis, it has been proposed that a three-segmented head in Fuxianhuia corresponds to a three-segmented brain as an ancestral state for Deuteropoda [17], composed of proto-, deuto- and tritocerebral segments. We caution, however, that the head segmentation of Fuxianhuia is under dispute, with evidence that taxa once viewed as having a comparable three-segmented head, such as Branchiocaris [92], later being shown to have mandibles and post-mandibular mouthparts [61]. Evo-devo work shows that there is a distinct difference between the way in which the anterior three segments (the pre-gnathal segments) are patterned in all extant arthropods relative to more posterior segments (figure 5). This is true in insects [48,95,96] and myriapods [93], which have a six-segmented head, and in chelicerates [94], which have a complex cephalothorax (prosoma) rather than a distinct head. Differences include a lack of involvement of pair-rule genes and a different regulation of segment polarity genes in the anterior segments (known from Drosophila [97], reviewed in [96]), lack of Hox gene expression in the anterior two segments [80], and an unusual mode of segment generation, which involves segmental genes being expressed in single stripes or patches in the pre-gnathal domain and then splitting to give two or three stripes that correspond to individual segments [48,93,94]. There is also some evidence for differences in the expression of segment polarity genes in these anterior segments in several species, but this has not been analysed in sufficient detail. Examples of anterior segmentation through 'stripe-splitting' in different arthropod taxa. (a,b) Blastoderm stages of the milkweed bug Oncopeltus fasciatus (Insecta). An anterior patch of wingless expression representing both the ocular (oc) and antennal (an) segment splits to give rise to two distinct expression domains. (c,d) Early development of the centipede Strigamia maritima (Myriapoda), showing the expression of hedgehog. The anterior expression stripe representing the ocular segment (blue arrow) splits first from a preliminary single stripe. This is followed by the separation of the antennal (green arrow) and intercalary (yellow arrow) segmental stripes. The expression stripe representing the mandibular segment (red arrow) appears independently. (e–g) Early germband embryo of the spider Parasteatoda tepidariorum (Chelicerata), showing expression of hedgehog (blue stain) and deformed (orange stain). The anterior expression of hedgehog starts as a single stripe, which splits once to give a stripe representing the pedipalpal segment (Pp) and a second stripe that soon splits again to give the stripes representing the ocular segment (Ce, cephalic lobe) and the cheliceral segment (Ch). Adapted (a,b) from [48], (c,d) from [93] and (e–g) from [94]. (Online version in colour.)We suggest that the unusual three anterior segments in extant arthropods represent the ancestral three-segment head found in Cambrian taxa that are near or within the arthropod crown-group. Under this hypothesis, the ancestral head segments were already developmentally distinct from the trunk segments at the time of their first appearance, and this difference has been maintained throughout their evolutionary history. It is still seen in all extant arthropods, as well as in Cambrian larvae that provide evidence for simultaneously developing head segments (a so-called 'head larva') being an ancestral character of crown-group arthropods [23]. This interpretation, which relies on combined data from fossils and embryos, provides a developmental-mechanistic scenario for the evolution of the three-segmented head from an ancestral single-segment head. Metameric gut diverticula are a common character in many stem-group arthropods. Based on the typical restriction of these diverticula to the posterior part of the head and the anterior part of the trunk (or much of the length of the trunk) versus a tube-shaped gut more anteriorly and posteriorly, the diverticula provide a basis for distinguishing the midgut from the foregut and hindgut in fossils. The midgut was strongly segmented in the arthropod stem-group (figure 6 [66,98]), including in the 'gilled lobopodians' (figure 6a,b) and isoxyids (figure 6c), as well as in some groups that have been interpreted as either stem-group or crown-group arthropods, such as megacheiran 'great appendage arthropods' (figure 6d) and trilobitomorphs (figure 6e,f). Throughout this evolutionary grade, the morphology of the midgut diverticula is conserved, being relatively large, reniform organs with a distinctive radiating canal system, underpinning their homology. This hypothesis that the gut was segmented at the origin of arthropods (the diverticula being present in giant lobopodians such as Jianshanopodia [98]) could only be formulated based on information from fossils, because gut segmentation is almost non-existent in extant arthropods. An exception to this are remipedes, which are unique in having paired segmental midgut diverticula, up to 32 pairs along the length of the midgut [98]. However, the deeply nested systematic position of remipedes within Pancrustacea (as sister group of hexapods) negates the possibility that their serially repeated midgut diverticula are a plesiomorphy retained from the arthropod stem-group. Segmental midgut diverticula (mgd) in Cambrian total-group Arthropoda. (a,b) The 'gilled lobopodian' Pambdelurion whittingtoni, scales 20 mm; (c) the isoxyid Isoxys acutangulus, scale 5 mm; (d) the megacheiran Leanchoilia superlata, scale 5 mm; (e,f) the trilobitomorph Kuamaia lata: left side of thorax, showing exopod flap (ef,) lamellar setae (ls) and diverticula on three segments, scales: (e) 2 mm and (f), 5 mm. (Online version in colour.)We cannot directly study the developmental origin of midgut segmentation, as we have no extant examples that are experimentally tractable. However, we can gain insights from what we know about germ layers in segmentation of arthropod laboratory models. All other metameric organ systems originate from undifferentiated mesoderm and ectoderm segmental precursors, which do not normally contribute to endodermal structures at all [99,100]. It is possible that the endodermal structures are 'entrained' to ectodermal or mesodermal structures, and thus their segmentation is secondary. This is in agreement with the model presented above for the evolution of segmental integration [4], which suggests that metamerism in different structures may have evolved independently and was secondarily integrated. Midgut diverticula could be an example of an individually metameric organ system that was not recruited into the main segmentation process and was thus more easily lost. Palaeontology provides novel evidence that in some fossil taxa dorsal ectodermal and endodermal structures (tergites and midgut diverticula, respectively) are matched segmentally, but they are out of synchronization with the ganglia of the ventral nerve cord and limbs (which are in turn in segmentally matched to each other). This is evidenced by the distribution of midgut diverticula in the fuxianhiiid Fuxianhuia protensa, which has one pair of diverticula matched to each of its anterior, appendage-bearing trunk segments [101]. It has long been known that fuxianhuiids have many more trunk appendages than tergites [91], and the discovery of the ventral nerve cord in the trunk of the fuxianhuiid Chengjiangocaris kunmingensis showed that ganglia of the nerve cord correspond to the distribution of appendages [102]. The regular, alternating pattern of terminal tergite addition and shedding of abdominal tergites into the thorax in Fuxianhuia, described above, has been interpreted as tergal formation corresponding to a general/primitive arthropod pattern versus a decoupled and phylogenetically derived mode of appendage development [82]. Fuxianhuiids are thus potentially relevant to discussion about dorsoventral decoupling in arthropods more generally [101], or lack of integration of different organ systems into one segmentation system. We must clarify that regardless of fuxianhuiids' exact position (in the arthropod crown-group or in the stem), they probably lost integration rather than displaying an ancestral unintegrated state. This type of mismatch has taken place several times throughout arthropod evolution, and is found both in fossil and extant taxa [103]. These observations about character covariation in fossils could inspire experiments that look at genetic linkages between segmentation mechanisms in the tergites and gut systems and at the possible role of re-segmentation in defining the position of different structures in (extant) model systems [104]. From the perspective of evo-devo, aspects of dorsoventral decoupling have been explored in some detail in millipedes, particularly using Glomeris marginata as a model for gene expression [39,105]. At the level of segment polarity gene expression, the ventral side of the embryo (e.g. sternites and legs) in G. marginata corresponds to patterns seen in other arthropods, whereas dorsal segmentation deviates in many respects. Dorsoventral developmental mismatch is also known from the branchiopod Triops [106] but in much less detail. Dorsal and ventral decoupling of segmentation is manifest even at the level of delimiting the posterior boundary of the head, which conspicuously differs in various groups (reviewed in [107]). The adult dorsoventral axis is represented in the germ band as a medio-lateral axis [108], and the mismatch can easily take place through changes in patterning during the germband stage. A comparative developmental approach to patterning along the dorsoventral axis of the germ band, with the level of segmental mismatch known from the fossil record as a reference point, should be highly informative for understanding the conservation or lability of developmental integration among the units that make up a segment. There are groups for which evo-devo gives us an understanding of segmental mechanisms (such as Hexapoda—informed by such models as Drosophila melanogaster and Tribolium castaneum) but palaeontology provides limited insights because key regions of tree space (such as the hexapod stem-group) are essentially unsampled. Conversely, there are other groups for which palaeontology gives us insights into the acquisition of segmental features, such as the arthropod stem-group (examples above) and the chelicerate stem-group, but evo-devo is challenged because extant taxa with features of interest are separated from their closest living relative by long branches, i.e. they have been subjected to so many evolutionary steps that understanding character evolution is difficult. Fossil chelicerates, for example, provide evidence of unique patterns of tagmosis that are not retained by extant forms, yet are critical to inferring ancestral states. Thus, stem-group 'synziphosurine' euchelicerates depict a combination of a shield-like prosoma, an articulated set of opisthosomal tergites and a tail spine [83]. As outlined in the examples above, the fossil record gives us a ‘search image’ for features to look for in comparative embryology, e.g. endodermal segmental characters force a rethink of how segments could have been generated ancestrally. It provides a possible explanation for patterns seen in development, such as pre-gnathal segments. Fossils also supply direct ontogenetic data for parts of tree space that are not represented by living taxa. Wholly extinct groups like trilobites, for example, allow for quantitative tree-based analysis of modes of trunk segmentation [109]. Lastly, palaeontology informs on rates of evolution of features of interest from an evo-devo perspective. This is most powerfully understood in the context of molecular time-trees calibrated by fossils, which constrain the origin of many segmental traits in arthropods to a window of time spanning the terminal Ediacaran and the Terreneuvian Series of the Cambrian [51,58,110–112]. Conversely, evo-devo provides mechanistic explanations for phenomena we observe in the fossils. It also raises hypotheses (e.g. germband reconstructions [108]) about the possible sequence of evolutionary events, which can potentially be corroborated by the fossil record, e.g. gradual integration of metameric systems into coherent segments. Evo-devo also provides linkages between different characters through identification of gene pleiotropies and developmental integration—neither of which are obvious from fossils or from general morphology. The two disciplines operate under different conceptual frameworks. These are partly overlapping (notably, both are fundamentally rooted in tree thinking), but each has much to learn from the other. Looking forward, many of the conflicts in recent phylogenetic trees aiming to place early derived fossil arthropods stem from differing interpretations of fossilized morphology. Burgess Shale-type fossils, as exquisite as they can be, are afflicted by taphonomy (decay, compaction, fragmentation, patchy mineralization, etc.), and teasing apart original anatomy and taphonomic artefacts is often complicated. In spite of this, improved imaging tools are allowing palaeontologists to extract more information from fossils. Arthropod compression fossils have for some years been productively investigated using polarized light and/or immersion in liquid [113], but have more recently provided additional data using such approaches as fluorescence microscopy [114], laminography [115] and computed micro-tomography [116]. These techniques may resolve some of the current controversies about homologies in fossil taxa that complicate character coding. The future also holds the prospect of genomic sequences as an additional source of information for understanding the evolution of morphology. A continued improvement in taxon sampling and an increased quality of genome sequencing and genome annotation will allow us to look for molecular signatures of developmental innovations within a phylogenetic framework. This will make it easier to generalize from the small sample of experimentally tractable species to species in under-sampled regions of the tree, and to possibly extrapolate to extinct taxa using our understanding of development from extant diversity. Finally, a glaring gap in current work on the evo-devo of segmentation can be potentially closed by bringing in insights from the fossil record. Most work on the development of segments focuses on the molecular processes leading to the undifferentiated segmental precursors. In terms of the segmental organization of the body, it is hardly an exaggeration to say that everything important has already happened by the germband stage and the expression of segment polarity genes. However, the morphology that is under selection, and which we see varying in the diversity of arthropods and their extinct relatives, is manifested later. The differentiation of repeated units of different systems within the segmental precursor has hardly been explored. This significant gap can be closed by focusing attention on later stages in development. A research agenda aimed at understanding the later stages and their diversity that takes advantage of genomic datasets and that integrates with the fossil record, which is for the most part post-embryonic, has the potential to paint a much more complete and nuanced picture of the evolution of the arthropod segmented body plan.

For fossil images, we thank Allison Daley, Diego García-Bellido, Jakob Vinther and the Royal Ontario Museum. For embryo images, we thank Michael Akam and Hiroki Oda. This article has no additional data. A.D.C. and G.D.E. conceived the study, wrote the manuscript and prepared the figures. We declare no competing interests. We received no funding for this study.

1.Chipman AD, Erwin DH. 2017. The evolution of arthropod body plans: integrating phylogeny, fossils, and development—an introduction to the symposium. Integr. Comp. Biol. 57, 450–454. (10.1093/icb/icx094) [DOI] [PubMed] [Google Scholar] 2.Edgecombe GD, Legg DA. 2013. The arthropod fossil record. In Arthropod biology and evolution (eds Minelli A, Boxshall G, Fusco G), pp. 393–415. Berlin, Germany: Springer. [Google Scholar] 3.Chipman AD. 2010. Parallel evolution of segmentation by co-option of ancestral gene regulatory networks. Bioessays 32, 60–70. (10.1002/bies.200900130) [DOI] [PubMed] [Google Scholar] 4.Chipman AD. 2019. Becoming segmented. In Perspectives on evolutionary developmental biology (ed. Fusco G.), pp. 235–244. Padova, Italy: Padova University Press. [Google Scholar] 5.Shubin N, Tabin C, Carroll S. 1997. Fossils, genes and the evolution of animal limbs. Nature 388, 639–648. (10.1038/41710) [DOI] [PubMed] [Google Scholar] 6.Coates MI. 1994. The origin of vertebrate limbs. Dev. Suppl. 1994, 169–180. [PubMed] [Google Scholar] 7.Coates MI, Cohn MJ. 1998. Fins, limbs and tails: outgrowths and axial patterning in vertebrate evolution. Bioessays 20, 371–381. () [DOI] [Google Scholar] 8.Patel NH, Kornberg TB, Goodman CS. 1989. Expression of engrailed during segmentation in grasshopper and crayfish. Development 107, 201–212. [DOI] [PubMed] [Google Scholar] 9.Patel NH, Ball EE, Goodman CS. 1992. Changing role of even-skipped during the evolution of insect pattern formation. Nature 357, 339–342. (10.1038/357339a0) [DOI] [PubMed] [Google Scholar] 10.Patel NH. 1994. The evolution of arthropod segmentation: insights from comparisons of gene expression patterns. Dev. Suppl. 1994, 201–207. (10.1016/0168-9525(89)90183-2) [DOI] [PubMed] [Google Scholar] 11.Akam M, Averof M, Castelli-Gair J, Dawes R, Falciani F, Ferrier D. 1994. The evolving role of Hox genes in arthropods. Dev. Suppl. 1994, 209–215. [PubMed] [Google Scholar] 12.Akam M. 1995. Hox genes and the evolution of diverse body plans. Phil. Trans. R. Soc. Lond. B 349, 313–319. (10.1098/rstb.1995.0119) [DOI] [PubMed] [Google Scholar] 13.Rogers BT, Kaufman TC. 1997. Structure of the insect head in ontogeny and phylogeny: a view from Drosophila. Int. Rev. Cytol. 174, 1–84. (10.1016/S0074-7696(08)62115-4) [DOI] [PubMed] [Google Scholar] 14.Rogers BT, Peterson MD, Kaufman TC. 1997. Evolution of the insect body plan as revealed by the Sex combs reduced expression pattern. Development 124, 149–157. [DOI] [PubMed] [Google Scholar] 15.Engel MS, Davis SR, Prokop J. 2013. Insect wings: the evolutionary development of nature's first fliers. In Arthropod biology and evolution (eds Minelli A, Boxshall G, Fusco G), pp. 269–298. Berlin, Germany: Springer. [Google Scholar] 16.Prokop J, Pecharova M, Nel A, Hornschemeyer T, Krzeminska E, Krzeminski W, Engel MS. 2017. Paleozoic nymphal wing pads support dual model of insect wing origins. Curr. Biol. 27, 263–269. (10.1016/j.cub.2016.11.021) [DOI] [PubMed] [Google Scholar] 17.Ortega-Hernández J, Janssen R, Budd GE. 2017. Origin and evolution of the panarthropod head: a palaeobiological and developmental perspective. Arthropod. Struct. Dev. 46, 354–379. (10.1016/j.asd.2016.10.011) [DOI] [PubMed] [Google Scholar] 18.Jockusch EL. 2017. Developmental and evolutionary perspectives on the origin and diversification of arthropod appendages. Integr. Comp. Biol. 57, 533–545. (10.1093/icb/icx063) [DOI] [PubMed] [Google Scholar] 19.Hughes NC, Hong PS, Hou JB, Fusco G. 2017. The development of the Silurian trilobite Aulacopleura koninckii reconstructed by applying inferred growth and segmentation dynamics: a case study in paleo-evo-devo. Front. Ecol. Evol. 5, 37 (10.3389/fevo.2017.00037) [DOI] [Google Scholar] 20.Fu DJ, et al. 2019. The Qingjiang biota-a Burgess Shale-type fossil Lagerstätte from the early Cambrian of South China. Science 363, 1338–1342. (10.1126/science.aau8800) [DOI] [PubMed] [Google Scholar] 21.Butterfield NJ, Harvey THP. 2012. Small carbonaceous fossils (SCFs): a new measure of early Paleozoic paleobiology. Geol. 40, 71–74. (10.1130/G32580.1) [DOI] [Google Scholar] 22.Maas A, et al. 2006. The ‘Orsten’—more than a Cambrian Konservat-Lagerstätte yielding exceptional preservation. Palaeoworld 15, 266–282. (10.1016/j.palwor.2006.10.005) [DOI] [Google Scholar] 23.Waloszek D, Maas A. 2005. The evolutionary history of crustacean segmentation: a fossil-based perspective. Evol. Dev. 7, 515–527. (10.1111/j.1525-142X.2005.05056.x) [DOI] [PubMed] [Google Scholar] 24.Haug JT, Maas A, Waloszek D. 2010. Henningsmoenicaris scutula, Sandtorpia vestrogothiensis gen. et sp nov and heterochronic events in early crustacean evolution. Earth Environ. Sci. Trans. R. Soc. Edinb. 100, 311–350. (10.1017/s1755691010008145) [DOI] [Google Scholar] 25.Chipman AD. 2017. Oncopeltus fasciatus as an evo-devo research organism. Genesis e23020 (10.1002/dvg.23020) [DOI] [PubMed] 26.Toubiana W, Khila A. 2016. The benefits of expanding studies of trait exaggeration to hemimetabolous insects and beyond morphology. Curr. Opin. Genet. Dev. 39, 14–20. (10.1016/j.gde.2016.05.015) [DOI] [PubMed] [Google Scholar] 27.McGregor AP, Hilbrant M, Pechmann M, Schwager EE, Prpic NM, Damen WGM. 2008. Cupiennius salei and Achaearanea tepidariorum: spider models for investigating evolution and development. Bioessays 30, 487–498. (10.1002/bies.20744) [DOI] [PubMed] [Google Scholar] 28.Leite DJ, McGregor AP. 2016. Arthropod evolution and development: recent insights from chelicerates and myriapods. Curr. Opin. Genet. Dev. 39, 93–100. (10.1016/j.gde.2016.06.002) [DOI] [PubMed] [Google Scholar] 29.Sharma PP, Schwager EE, Extavour CG, Giribet G. 2012. Hox gene expression in the harvestman Phalangium opilio reveals divergent patterning of the chelicerate opisthosoma. Evol. Dev. 14, 450–463. (10.1111/j.1525-142X.2012.00565.x) [DOI] [PubMed] [Google Scholar] 30.Sharma PP. 2017. Chelicerates and the conquest of land: a view of arachnid origins through an evo-devo spyglass. Integr. Comp. Biol. 57, 510–522. (10.1093/icb/icx078) [DOI] [PubMed] [Google Scholar] 31.Stauber M, Taubert H, Schmidt-Ott U. 2000. Function of bicoid and hunchback homologs in the basal cyclorrhaphan fly Megaselia (Phoridae). Proc. Natl Acad. Sci. USA 97, 10 844–10 849. (10.1073/pnas.190095397) [DOI] [PMC free article] [PubMed] [Google Scholar] 32.Schmidt-Ott U, Lynch JA. 2016. Emerging developmental genetic model systems in holometabolous insects. Curr. Opin. Genet. Dev. 39, 116–128. (10.1016/j.gde.2016.06.004) [DOI] [PubMed] [Google Scholar] 33.García-Solache M, Jaeger J, Akam M. 2010. A systematic analysis of the gap gene system in the moth midge Clogmia albipunctata. Dev. Biol. 344, 306–318. (10.1016/j.ydbio.2010.04.019) [DOI] [PubMed] [Google Scholar] 34.Cicin-Sain D, Pulido AH, Crombach A, Wotton KR, Jiménez-Guri E, Taly JF, Roma G, Jaeger J. 2015. SuperFly: a comparative database for quantified spatio-temporal gene expression patterns in early dipteran embryos. Nuc. Acids Res. 43, D751–D755. (10.1093/nar/gku1142) [DOI] [PMC free article] [PubMed] [Google Scholar] 35.Pavlopoulos A, Averof M. 2005. Establishing genetic transformation for comparative developmental studies in the crustacean Parhyale hawaiensis. Proc. Natl Acad. Sci. USA 102, 7888–7893. (10.1073/pnas.0501101102) [DOI] [PMC free article] [PubMed] [Google Scholar] 36.Eriksson BJ, Ungerer P, Stollewerk A. 2013. The function of Notch signalling in segment formation in the crustacean Daphnia magna (Branchiopoda). Dev. Biol. 383, 321–330. (10.1016/j.ydbio.2013.09.021) [DOI] [PubMed] [Google Scholar] 37.Sun DA, Patel NH. 2019. The amphipod crustacean Parhyale hawaiensis: an emerging comparative model of arthropod development, evolution, and regeneration. Wiley Interdiscip. Rev. Dev. Biol. 8, e355 (10.1002/wdev.355) [DOI] [PMC free article] [PubMed] [Google Scholar] 38.Arthur W, Chipman AD. 2005. The centipede Strigamia maritima: what it can tell us about the development and evolution of segmentation. Bioessays 27, 653–660. (10.1002/bies.20234) [DOI] [PubMed] [Google Scholar] 39.Janssen R, Prpic N-M, Damen WGM. 2004. Gene expression suggests decoupled dorsal and ventral segmentation in the millipede Glomeris marginata (Myriapoda : Diplopoda). Dev. Biol. 268, 89–104. (10.1016/j.ydbio.2003.12.021) [DOI] [PubMed] [Google Scholar] 40.Medved V, Marden JH, Fescemyer HW, Der JP, Liu J, Mahfooz N, Popadic A. 2015. Origin and diversification of wings: insights from a neopteran insect. Proc. Natl Acad. Sci. USA 112, 15 946–15 951. (10.1073/pnas.1509517112) [DOI] [PMC free article] [PubMed] [Google Scholar] 41.Clark-Hachtel CM, Tomoyasu Y. 2016. Exploring the origin of insect wings from an evo-devo perspective. Curr. Opin. Insect Sci. 13, 77–85. (10.1016/j.cois.2015.12.005) [DOI] [PubMed] [Google Scholar] 42.Thomas GWC, et al. 2019. The genomic basis of arthropod diversity. bioRxiv (10.1101/382945) [DOI] [Google Scholar] 43.Chipman AD, Arthur W, Akam M. 2004. Early development and segment formation in the centipede Strigamia maritima (Geophilomorpha). Evol. Dev. 6, 78–89. (10.1111/j.1525-142X.2004.04016.x) [DOI] [PubMed] [Google Scholar] 44.Choe CP, Miller SC, Brown SJ. 2006. A pair-rule gene circuit defines segments sequentially in the short-germ insect Tribolium castaneum. Proc. Natl Acad. Sci. USA 103, 6560–6564. (10.1073/pnas.0510440103) [DOI] [PMC free article] [PubMed] [Google Scholar] 45.Janssen R. 2012. Segment polarity gene expression in a myriapod reveals conserved and diverged aspects of early head patterning in arthropods. Dev. Genes Evol. 222, 299–309. (10.1007/s00427-012-0413-9) [DOI] [PubMed] [Google Scholar] 46.Brena C, Akam M. 2013. An analysis of segmentation dynamics throughout embryogenesis in the centipede Strigamia maritima. BMC Biol. 11, 112 (10.1186/1741-7007-11-112) [DOI] [PMC free article] [PubMed] [Google Scholar] 47.Schönauer A, Paese CL, Hilbrant M, Leite DJ, Schwager EE, Feitosa NM, Eibner C, Damen WG, McGregor AP. 2016. The Wnt and Delta-Notch signalling pathways interact to direct pair-rule gene expression via caudal during segment addition in the spider Parasteatoda tepidariorum. Development 143, 2455–2463. (10.1242/dev.131656) [DOI] [PubMed] [Google Scholar] 48.Stahi R, Chipman AD. 2016. Blastoderm segmentation in Oncopeltus fasciatus and the evolution of arthropod segmentation mechanisms. Proc. R. Soc. B 283, 20161745 (10.1098/rspb.2016.1745) [DOI] [PMC free article] [PubMed] [Google Scholar] 49.Auman T, Chipman AD. 2018. Growth zone segmentation in the milkweed bug Oncopeltus fasciatus sheds light on the evolution of insect segmentation. BMC Evol. Biol. 18, 178 (10.1186/s12862-018-1293-z) [DOI] [PMC free article] [PubMed] [Google Scholar] 50.Giribet G, Edgecombe GD. 2019. The phylogeny and evolutionary history of arthropods. Curr. Biol. 29, R592–R602. (10.1016/j.cub.2019.04.057) [DOI] [PubMed] [Google Scholar] 51.Misof B, et al. 2014. Phylogenomics resolves the timing and pattern of insect evolution. Science 346, 763–767. (10.1126/science.1257570) [DOI] [PubMed] [Google Scholar] 52.Schwentner M, Combosch DJ, Pakes Nelson J, Giribet G. 2017. A phylogenomic solution to the origin of insects by resolving crustacean-hexapod relationships. Curr. Biol. 27, 1818–1824. (10.1016/j.cub.2017.05.040) [DOI] [PubMed] [Google Scholar] 53.Lozano-Fernandez J, et al. 2019. Pancrustacean evolution illuminated by taxon-rich genomic-scale data sets with an expanded remipede sampling. Genome Biol. Evol. 11, 2055–2070. (10.1093/gbe/evz097) [DOI] [PMC free article] [PubMed] [Google Scholar] 54.Fernández R, Laumer CE, Vahtera V, Libro S, Kaluziak S, Sharma PP, Perez-Porro AR, Edgecombe GD, Giribet G. 2014. Evaluating topological conflict in centipede phylogeny using transcriptomic data sets. Mol. Biol. Evol. 31, 1500–1513. (10.1093/molbev/msu108) [DOI] [PubMed] [Google Scholar] 55.Fernández R, Edgecombe GD, Giribet G. 2018. Phylogenomics illuminates the backbone of the Myriapoda Tree of Life and reconciles morphological and molecular phylogenies. Sci. Rep. 8, 83 (10.1038/s41598-017-18562-w) [DOI] [PMC free article] [PubMed] [Google Scholar] 56.Lozano-Fernandez J, Tanner AR, Giacomelli M, Carton R, Vinther J, Edgecombe GD, Pisani D. 2019. Increasing species sampling in chelicerate genomic-scale datasets provides support for monophyly of Acari and Arachnida. Nat. Commun. 10, 2295 (10.1038/s41467-019-10244-7) [DOI] [PMC free article] [PubMed] [Google Scholar] 57.Ballesteros JA, Sharma PP. In press A critical appraisal of the placement of Xiphosura (Chelicerata) with account of known sources of phylogenetic error. Syst. Biol. (10.1093/sysbio/syz011) [DOI] [PubMed] [Google Scholar] 58.Daley AC, Antcliffe JB, Drage HB, Pates S. 2018. Early fossil record of Euarthropoda and the Cambrian Explosion. Proc. Natl Acad. Sci. USA 115, 5323–5331. (10.1073/pnas.1719962115) [DOI] [PMC free article] [PubMed] [Google Scholar] 59.Legg DA, Vannier J. 2013. The affinities of the cosmopolitan arthropod Isoxys and its implications for the origin of arthropods. Lethaia 46, 540–550. (10.1111/let.12032) [DOI] [Google Scholar] 60.Yang J, Ortega-Hernández J, Legg DA, Lan T, Hou JB, Zhang XG. 2018. Early Cambrian fuxianhuiids from China reveal origin of the gnathobasic protopodite in euarthropods. Nat. Commun. 9, 470. [DOI] [PMC free article] [PubMed] [Google Scholar] 61.Aria C, Caron JB. 2017. Burgess Shale fossils illustrate the origin of the mandibulate body plan. Nature 545, 89–92. (10.1038/nature22080) [DOI] [PubMed] [Google Scholar] 62.Vannier J, Aria C, Taylor RS, Caron JB. 2018. Waptia fieldensis Walcott, a mandibulate arthropod from the middle Cambrian Burgess Shale. R. Soc. open sci. 5 (10.1098/rsos.172206) [DOI] [PMC free article] [PubMed] [Google Scholar] 63.Liu JN, Shu D, Han J, Zhang ZF, Zhang XL. 2006. A large xenusiid lobopod with complex appendages from the Lower Cambrian Chengjiang Lagerstatte. Acta Palaeontol. Pol. 51, 215–222. [Google Scholar] 64.Liu JN, Shu DG, Han J, Zhang ZF, Zhang XL. 2007. Morpho-anatomy of the lobopod Magadictyon cf. haikouensis from the Early Cambrian Chengjiang Lagerstatte, South China. Acta Zool. 88, 279–288. (10.1111/j.1463-6395.2007.00281.x) [DOI] [Google Scholar] 65.Dzik J. 2011. The xenusian-to-anomalocaridid transition within the lobopodians. B. Soc. Paleontol. Ital. 50, 65–74. [Google Scholar] 66.Daley AC, Edgecombe GD. 2014. Morphology of Anomalocaris canadensis from the Burgess Shale. J. Paleont. 88, 68–91. (10.1666/13-067) [DOI] [Google Scholar] 67.Park TS, et al. 2018. Brain and eyes of Kerygmachela reveal protocerebral ancestry of the panarthropod head. Nat. Commun. 9, 1019 (10.1038/s41467-018-03464-w) [DOI] [PMC free article] [PubMed] [Google Scholar] 68.Daley AC, Budd GE, Caron JB, Edgecombe GD, Collins D. 2009. The Burgess Shale anomalocaridid Hurdia and its significance for early euarthropod evolution. Science 323, 1597–1600. (10.1126/science.1169514) [DOI] [PubMed] [Google Scholar] 69.Van Roy P, Daley AC, Briggs DE. 2015. Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps. Nature 522, 77–80. (10.1038/nature14256) [DOI] [PubMed] [Google Scholar] 70.Jockusch EL, Smith FW. 2015. Hexapoda: comparative aspects of later embryogenesis and development. In Evolutionary developmental biology of invertebrates (ed. Wanninger A.), pp. 111–208. Vienna, Austria: Springer. [Google Scholar] 71.Janssen R, Eriksson BJ, Budd GE, Akam M, Prpic NM. 2010. Gene expression patterns in an onychophoran reveal that regionalization predates limb segmentation in pan-arthropods. Evol. Dev. 12, 363–372. (10.1111/j.1525-142X.2010.00423.x) [DOI] [PubMed] [Google Scholar] 72.Janssen R, Jorgensen M, Prpic NM, Budd GE. 2015. Aspects of dorso-ventral and proximo-distal limb patterning in onychophorans. Evol. Dev. 17, 21–33. (10.1111/ede.12107) [DOI] [PubMed] [Google Scholar] 73.Ortega-Hernández J. 2016. Making sense of ‘lower’ and ‘upper’ stem-group Euarthropoda, with comments on the strict use of the name Arthropoda von Siebold, 1848. Biol. Rev. Camb. Philos. Soc. 91, 255–273. (10.1111/brv.12168) [DOI] [PubMed] [Google Scholar] 74.Wagner GP. 2014. Homology, genes and evolutionary innovation. Princeton, NJ: Princeton University Press. [Google Scholar] 75.Arthur W, Jowett T, Panchen A. 1999. Segments, limbs, homology, and co-option. Evol. Dev. 1, 74–76. (10.1046/j.1525-142x.1999.98004.x) [DOI] [PubMed] [Google Scholar] 76.Ganfornina MD, Sanchez D. 1999. Generation of evolutionary novelty by functional shift. Bioessays 21, 432–439. () [DOI] [PubMed] [Google Scholar] 77.Shubin N, Tabin C, Carroll S. 2009. Deep homology and the origins of evolutionary novelty. Nature 457, 818–823. (10.1038/nature07891) [DOI] [PubMed] [Google Scholar] 78.Peterson T, Müller GB. 2013. What is evolutionary novelty? Process versus character based definitions. J. Exp. Zool. B 320, 345–350. (10.1002/jez.b.22508) [DOI] [PubMed] [Google Scholar] 79.Panganiban G, Nagy L, Carroll SB. 1994. The role of the Distal-less gene in the development and evolution of insect limbs. Curr. Biol. 4, 671–675. (10.1016/S0960-9822(00)00151-2) [DOI] [PubMed] [Google Scholar] 80.Hughes CL, Kaufman TC. 2002. Hox genes and the evolution of the arthropod body plan. Evol. Dev. 4, 459–499. (10.1046/j.1525-142X.2002.02034.x) [DOI] [PubMed] [Google Scholar] 81.Auman T, Chipman AD. 2017. The evolution of gene regulatory networks that define arthropod body plans. Integr. Comp. Biol. 57, 523–532. (10.1093/icb/icx035) [DOI] [PubMed] [Google Scholar] 82.Fu D, Ortega-Hernandez J, Daley AC, Zhang X, Shu D. 2018. Anamorphic development and extended parental care in a 520 million-year-old stem-group euarthropod from China. BMC Evol. Biol. 18, 147 (10.1186/s12862-018-1262-6) [DOI] [PMC free article] [PubMed] [Google Scholar] 83.Dunlop JA, Lamsdell JC. 2017. Segmentation and tagmosis in Chelicerata. Arthropod Struct. Dev. 46, 395–418. (10.1016/j.asd.2016.05.002) [DOI] [PubMed] [Google Scholar] 84.Miyawaki K, Mito T, Sarashina I, Zhang HJ, Shinmyo Y, Ohuchi H, Noji S. 2004. Involvement of Wingless/Armadillo signaling in the posterior sequential segmentation in the cricket, Gryllus bimaculatus (Orthoptera), as revealed by RNAi analysis. Mech. Dev. 121, 119–130. (10.1016/j.mod.2004.01.002) [DOI] [PubMed] [Google Scholar] 85.McGregor AP, Pechmann M, Schwager EE, Feitosa NM, Kruck S, Aranda M, Damen WG. 2008. Wnt8 is required for growth-zone establishment and development of opisthosomal segments in a spider. Curr. Biol. 18, 1619–1623. (10.1016/j.cub.2008.08.045) [DOI] [PubMed] [Google Scholar] 86.Mittmann B, Wolff C. 2012. Embryonic development and staging of the cobweb spider Parasteatoda tepidariorum C. L. Koch, 1841 (syn.: Achaearanea tepidariorum; Araneomorphae; Theridiidae). Dev. Genes Evol. 222, 189–216. (10.1007/s00427-012-0401-0) [DOI] [PubMed] [Google Scholar] 87.Dearden PK, Donly C, Grbic M. 2002. Expression of pair-rule gene homologues in a chelicerate: early patterning of the two-spotted spider mite Tetranychus urticae. Development 129, 5461–5472. (10.1242/dev.00099) [DOI] [PubMed] [Google Scholar] 88.Smith FW, Bartels PJ, Goldstein B. 2017. A hypothesis for the composition of the tardigrade brain and its implications for panarthropod brain evolution. Integr. Comp. Biol. 57, 546–559. (10.1093/icb/icx081) [DOI] [PubMed] [Google Scholar] 89.Mayer G, Kauschke S, Rüdiger J, Stevenson PA. 2013. Neural markers reveal a one-segmented head in tardigrades (water bears). PLoS ONE 8, e59090 (10.1371/journal.pone.0059090) [DOI] [PMC free article] [PubMed] [Google Scholar] 90.Cong PY, Edgecombe GD, Daley AC, Guo J, Pates S, Hou XG. 2018. New radiodonts with gnathobase-like structures from the Cambrian Chengjiang biota and implications for the systematics of Radiodonta. Pap. Palaeontol. 4, 605–621. (10.1002/spp2.1219) [DOI] [Google Scholar] 91.Chen JY, Edgecombe GD, Ramskold L, Zhou GQ. 1995. Head segmentation in Early Cambrian Fuxianhuia: implications for arthropod evolution. Science 268, 1339–1343. (10.1126/science.268.5215.1339) [DOI] [PubMed] [Google Scholar] 92.Budd GE. 2008. Head structure in upper stem-group euarthropods. Palaeontology 51, 561–573. (10.1111/j.1475-4983.2008.00752.x) [DOI] [Google Scholar] 93.Hunnekuhl VS, Akam M. 2017. Formation and subdivision of the head field in the centipede Strigamia maritima, as revealed by the expression of head gap gene orthologues and hedgehog dynamics. EvoDevo 8, 18 (10.1186/s13227-017-0082-x) [DOI] [PMC free article] [PubMed] [Google Scholar] 94.Kanayama M, Akiyama-Oda Y, Nishimura O, Tarui H, Agata K, Oda H. 2011. Travelling and splitting of a wave of hedgehog expression involved in spider-head segmentation. Nat. Commun. 2, 500 (10.1038/ncomms1510) [DOI] [PMC free article] [PubMed] [Google Scholar] 95.Posnien N, Bucher G. 2010. Formation of the insect head involves lateral contribution of the intercalary segment, which depends on Tc-labial function. Dev. Biol. 338, 107–116. (10.1016/j.ydbio.2009.11.010) [DOI] [PubMed] [Google Scholar] 96.Posnien N, Schinko JB, Kittelmann S, Bucher G. 2010. Genetics, development and composition of the insect head: a beetle's view. Arthropod. Struct. Dev. 39, 399–410. (10.1016/j.asd.2010.08.002) [DOI] [PubMed] [Google Scholar] 97.Gallitano-Mendel A, Finkelstein R. 1997. Novel segment polarity gene interactions during embryonic head development in Drosophila. Dev. Biol. 192, 599–613. (10.1006/dbio.1997.8753) [DOI] [PubMed] [Google Scholar] 98.Vannier J, Liu J, Lerosey-Aubril R, Vinther J, Daley AC. 2014. Sophisticated digestive systems in early arthropods. Nat. Commun. 5, 3641 (10.1038/ncomms4641) [DOI] [PubMed] [Google Scholar] 99.Hannibal RL, Price AL, Patel NH. 2012. The functional relationship between ectodermal and mesodermal segmentation the crustacean, Parhyale hawaiensis. Dev. Biol. 361, 427–438. (10.1016/j.ydbio.2011.09.033) [DOI] [PubMed] [Google Scholar] 100.Azpiazu N, Lawrence PA, Vincent JP, Frasch M. 1996. Segmentation and specification of the Drosophila mesoderm. Gene. Dev. 10, 3183–3194. (10.1101/gad.10.24.3183) [DOI] [PubMed] [Google Scholar] 101.Ortega-Hernández J, Fu D, Zhang X, Shu D. 2018. Gut glands illuminate trunk segmentation in Cambrian fuxianhuiids. Curr. Biol. 28, R146–R147. (10.1016/j.cub.2018.01.040) [DOI] [PubMed] [Google Scholar] 102.Yang J, Ortega-Hernández J, Butterfield NJ, Liu Y, Boyan GS, Hou JB, Lan T, Zhang XG. 2016. Fuxianhuiid ventral nerve cord and early nervous system evolution in Panarthropoda. Proc. Natl Acad. Sci. USA 113, 2988–2993. (10.1073/pnas.1522434113) [DOI] [PMC free article] [PubMed] [Google Scholar] 103.Ortega-Hernández J, Brena C. 2012. Ancestral patterning of tergite formation in a centipede suggests derived mode of trunk segmentation in trilobites. PLoS ONE 7, e52623 (10.1371/journal.pone.0052623) [DOI] [PMC free article] [PubMed] [Google Scholar] 104.Martínez-Arias A, Lawrence PA. 1985. Parasegments and compartments in the Drosophila embryo. Nature 313, 639–642. (10.1038/313639a0) [DOI] [PubMed] [Google Scholar] 105.Janssen R, Damen WGM. 2006. The ten Hox genes of the millipede Glomeris marginata. Dev. Genes Evol. 216, 451–465. (10.1007/s00427-006-0092-5) [DOI] [PubMed] [Google Scholar] 106.Nulsen C, Nagy LM. 1999. The role of wingless in the development of multibranched crustacean limbs. Dev. Genes. Evol. 209, 340–348. (10.1007/s004270050262) [DOI] [PubMed] [Google Scholar] 107.Scholtz G. 2015. Heads and brains in arthropods: 40 years after the ‘endless dispute’. In Structure and evolution of invertebrate nervous systems (eds Schmidt-Rhaesa A, Harzsch S, Purschke G), pp. 402–410. Oxford, UK: Oxford University Press. [Google Scholar] 108.Chipman AD. 2015. An embryological perspective on the early arthropod fossil record. BMC Evol. Biol. 15, 285 (10.1186/s12862-015-0566-z) [DOI] [PMC free article] [PubMed] [Google Scholar] 109.Fusco G, Garland T Jr, Hunt G, Hughes NC. 2012. Developmental trait evolution in trilobites. Evolution 66, 314–329. (10.1111/j.1558-5646.2011.01447.x) [DOI] [PubMed] [Google Scholar] 110.Rota-Stabelli O, Daley AC, Pisani D. 2013. Molecular timetrees reveal a Cambrian colonization of land and a new scenario for ecdysozoan evolution. Curr. Biol. 23, 392–398. (10.1016/j.cub.2013.01.026) [DOI] [PubMed] [Google Scholar] 111.Lozano-Fernandez J, et al. 2016. A molecular palaeobiological exploration of arthropod terrestrialization. Phil. Trans. R. Soc. B 371, 20150133 (10.1098/rstb.2015.0133) [DOI] [PMC free article] [PubMed] [Google Scholar] 112.Wolfe JM, Daley AC, Legg DA, Edgecombe GD. 2016. Fossil calibrations for the arthropod Tree of Life. Earth-Sci. Rev. 160, 43–110. (10.1016/j.earscirev.2016.06.008) [DOI] [Google Scholar] 113.Bengtson S. 2000. Teasing fossils out of shales with cameras and computers. Palaeo. Electron. 3, 4. [Google Scholar] 114.Haug JT, et al. 2011. Autofluorescence imaging, an excellent tool for comparative morphology. J. Microsc. 244, 259–722. (10.1111/j.1365-2818.2011.03534.x) [DOI] [PubMed] [Google Scholar] 115.Zuber M, Laass M, Hamann E, Kretschmer S, Hauschke N, van de Kamp T, Baumbach T, Koenig T.. 2017. Augmented laminography, a correlative 3D imaging method for revealing the inner structure of compressed fossils. Sci. Rep. 7, 41413 (10.1038/srep41413) [DOI] [PMC free article] [PubMed] [Google Scholar] 116.Zhai D, Ortega-Hernández J, Wolfe JM, Hou X, Cao C, Liu Y. 2019. Three-dimensionally preserved appendages in an Early Cambrian stem-group pancrustacean. Curr. Biol. 29, 171–177. (10.1016/j.cub.2018.11.060) [DOI] [PubMed] [Google Scholar]

In many arthropods, production and differentiation of new segments are not completed by the end of embryogenesis but continue, in different form and degree, well after hatching, in some cases up to the last post-embryonic molt. The post-embryonic addition of new segments is called anamorphosis and the taxa that present this mode of development are said to exhibit anamorphic development. Alternative to this developmental mode is epimorphic development, where the number of segments remains constant throughout the whole post-embryonic life. Completing the spectrum of options for the ontogenetic variation in the number of segments, there is the much less common process of desegmentation (or regressive segmentation), where the number of segments decreases at some point of the post-embryonic development; this is limited to a few holometabolous insects (Minelli and Fusco, 2013). Post-embryonic segment addition is not necessarily limited to a reproductively immature condition or to a larval phase, when present. Anamorphosis: Numbers and Modes Segmentation is a combination of multiple developmental processes that span from the first expression of segmentation genes to the complete display of all the morphological features of a mature segmental body unit. Since segmental units undergo developmental patterning (which may involve size, shape, limb formation, etc.), the “segmental stage” at which a segment can be considered “laid down” is an arbitrary choice. For instance, in the anostracan crustacean Artemia, this was identified either with the “segmental stage c,” at which the segment has the shape of a short cylinder (Weisz, 1946), or with the appearance of a stripe of Engrailed protein at the prospective posterior boundary of the segment (Williams et al., 2012). For our comparative purposes, we count as developmental addition of a new segment the first morphological appearance of a segmental unit as traditionally recognized by descriptive morphology (not necessarily the same for all taxa), irrespective of how close it is to its final morphology (e.g., disregarding presence/absence of limb buds). We calculated a degree of anamorphosis as the percentage of segments that are added during post-embryonic life, from 0% in epimorphic taxa, to >95% in the longest millipedes (see Supplementary Table 1 for details on segment count). Independent from the degree of anamorphosis, three main modes of anamorphosis are recognized, as first proposed by Enghoff et al. (1993) for millipedes. In euanamorphosis, segment number increases at each molt throughout the whole post-embryonic life, to terminate only with the death of the animal. In teloanamorphosis, segment number also increases throughout the animal's life, but both the number of molts and the schedule of segment addition at each molt are fixed for a given species and sex. Finally, in hemianamorphosis, the post-embryonic development includes a first anamorphic phase, through a first batch of stages (instars) separated by molts, followed by an epimorphic phase where molts take place without further increase in the number of body segments. Taxonomic Survey Anamorphosis in Extant Arthropods The distribution of anamorphosis and epimorphosis in the main groups is shown in Figure 1 (reference to source data in Supplementary Table 1). Figure 1. Phylogenetic distribution of segmentation modes in arthropods. Phylogeny based on Giribet and Edgecombe (2019), Chipman and Edgecombe (2019) (fossils), Howard et al. (2020) (Chelicerata), Fernández et al. (2016) (Myriapoda), and Schwentner et al. (2018) (Branchiopoda and Malacostraca). p, plesiomorphic condition; a, apomorphic condition; H, hemianamorphosis; T, teloanamorphosis; Eu, eunanamorphosis; Ep, epimorphosis; Epim., Epimorpha; Ecto., Ectognatha. Color of boxes and figures inside each box (percentage of body segments added post-embryonically) express the degree of anamorphosis (quantified only for extant taxa). In case of variation at lower taxonomic level, data refers to the most common or to the hypothesized plesiomorphic condition in the taxon. Details in Supplementary Table 1. In Chelicerata, hemianamorphosis is found among the Pycnogonida, which are sister to all the other Chelicerata, the Euchelicerata; these are all epimorphic to the exclusion of the Acariformes. Within the Pycnogonida and Acariformes, a few lineages have independently evolved epimorphic development (Lindquist, 1984; Brenneis and Arango, 2019). Most myriapod lineages are hemianamorphic. Epimorphic development only occurs in the centipede clade rightly named Epimorpha, which includes the Scolopendromorpha and Geophilomorpha. Euanamorphosis and teloanamorphosis are found among the Helminthomorpha millipedes exclusively, where both modes may have evolved once or several times independently (Miyazawa et al., 2014). Within the Pancrustacea, hemianamorphosis is the most common developmental mode among the “crustacean” (non-Hexapoda) lineages, but epimorphic development has evolved in some lineages, in association with direct development, whereas teloanamorphosis has possibly evolved in Copepoda (Huys, 2014) and euanamorphosis in Remipedia (Koenemann et al., 2009). Within the Hexapoda, only the Protura are hemianamorphic, while the Collembola, Diplura, and Insecta are epimorphic. Anamorphosis in Fossil Arthropods Ontogenetic series are available for several fossil arthropods, both stem- and crown-group. Many of these show anamorphic development and hemianamorphosis seems to be the most common mode of segmentation among stem-group taxa (e.g., Fu et al., 2014, 2018). However, segmentation in these ancient forms also exhibits some distinctive features with respect to extant taxa. Many Phosphatocopina, interpreted either as stem-group Pancrustacea (Haug and Haug, 2015) or stem-group Mandibulata (Chipman and Edgecombe, 2019), were anamorphic with indirect development (Haug and Haug, 2015), hatching as so-called head larva. In contrast to modern anamorphic taxa, no segments were added with the first few molts, that is, anamorphosis was in some way delayed. Another peculiar feature of anamorphosis in these early forms was that, similar to trilobites, segments first emerged as dorsally non-articulated units forming a single shield, the pygidium. The most anterior pygidial segments developed articulation in successive stages, in a process that in trilobites is called segment release. Trilobita, variably assigned to stem-group arthropods, stem-group chelicerates or stem-group mandibulates (Giribet and Edgecombe, 2019), mostly developed hemianamorphically (Hughes et al., 2006). However, some Emuellidae, with more than 100 trunk segments as adults, were possibly euanamorphic (Paterson and Edgecombe, 2006), whereas Zhang and Clarkson (2009) made the case for an epimorphic eodiscoid species. Delayed anamorphosis might have characterized trilobite post-embryonic development as well. Evidence for an even earlier phase of cephalic segment addition (during the so-called phaselus stage, if this was actually a phase of trilobite ontogeny), is weak (Hughes et al., 2006). Phylogenetic Patterns Phylogenetic distribution of anamorphosis in extant taxa and information from extinct forms concur to indicate hemianamorphic development as the primitive condition in arthropods (Hughes et al., 2006; Minelli and Fusco, 2013; Miyazawa et al., 2014; Haug and Haug, 2015; Brenneis et al., 2017). Uncertainties on key nodes of arthropod phylogeny and incomplete information on post-embryonic segmentation in several taxa prevent a formal analysis of the evolution of this developmental character at the level of the whole clade. However, starting from the hypothesis of hemianamorphosis as the plesiomorphic condition and complementing the phylogenetic distribution of the character in Figure 1 with some available information at lower taxonomic level, four different evolutionary transitions can be recognized. (i) Partial embryonization of segmentation (less anamorphic segments), with a consequent reduction in the degree of anamorphosis, seems to have occurred frequently. Millipedes usually have four trunk segments at hatching, but several species from different clades (Polyzoniida, Platydesmida, Julida, Stemmiulida, Spirobolida) hatch with more, up to 38 segments (Minelli, 2015; Supplementary Table 1). In centipedes, interpretation of the phylogenetic pattern crucially depends on the identity of the taxon that is sister to Epimorpha, either Lithobiomorpha or Craterostigmomorpha. In the first case, mainly supported by molecular data, from the primitive condition represented by Scutigeromorpha, there would have been a conspicuous embryonization of segmentation in Craterostigmomorpha firstly, followed by an opposite change in Lithobiomorpha and complete embryonization in Geophilomorpha. In the second case, mainly supported by morphological data (other than segmentation mode), a progressive embryonization from Scutigeromorpha to Epimorpha would have occurred. Among crustaceans, from a primitive condition of hatching as a nauplius larva, many lineages have independently evolved shorter anamorphic development, hatching as a more advanced-stage larva (e.g., metanauplius in Cephalocarida and Mystacocarida). This cannot generally be interpreted as a systemic heterochronic change, because different aspects of segmentation (segment appearance, segment patterning, or limb formation) and development of larval features (autonomous nutrition, locomotion, muscular, and nervous systems) are not necessarily associated (Fritsch et al., 2013; Haug and Haug, 2015; Jirikowski et al., 2015). Segmental patterning can even progress in the opposite direction with respect to segment addition, i.e., from posterior to anterior (Minelli, 2003, p. 162). (ii) Complete embryonization of segmentation (epimorphosis) has evolved several times independently: at least in one trilobite species (Zhang and Clarkson, 2009), in some lineages of Pycnogonida (Brenneis et al., 2017), in Euchelicerata, in Epimorpha among the centipedes, in several lineages of Malacostraca (but see below), in Cladocera and twice among the Hexapoda, i.e., in Collembola and Ectognatha. In some cases, this process is associated with the evolution of direct from indirect development (many crustaceans) and a shortening of the metameric trunk (e.g., Branchiura and Cladocera). However, the opposite is observed in Geophilomorpha, where epimorphosis is associated with the most segment-rich trunks among the arthropods. It must also be noted that epimorphosis can evolve from anamorphosis not only by embryonization of the addition of most posterior segments, but also from the suppression of the addition of those segments (suppressed anamorphosis), as suggested for some lineages of Acariformes (Bochkov, 2009; Bolton et al., 2017). (iii) Partial de-embryonization of sequential segmentation from an anamorphic condition (more segments produced by anamorphosis), with a consequent increase in the degree of anamorphosis, is apparently less common. Stem-group Pancrustacea hatched as head larvae of five segments, whereas the primitive condition for crown-group Pancrustacea is thought to be a four-segment nauplius (Haug and Haug, 2015). According to Scholtz (2000), Euphausiacea and Dendrobranchiata would have evolved a “new” nauplius secondarily (and in parallel) from primitive Malacostraca with shorter anamorphosis, but this has been questioned more recently (Akther et al., 2015; see also below). In centipedes, if Lithobiomorpha are actually sister to Epimorpha (see above), the former would have extended anamorphosis from a shorter Craterostigmomorpha-like condition. (iv) Partial de-embryonization of embryonic sequential segmentation from epimorphosis (secondary anamorphosis), seems to be even more rare, and putative cases are uncertain. In Pycnogonida, some Nymphonidae might have returned to anamorphosis (Brenneis et al., 2017), but uncertainties on the phylogeny of epimorphic pycnogonids do not allow to resolve this transition with confidence. If Euchelicerata are primitively epimorphic, Acariformes would have evolved anamorphosis secondarily. However, due to the persisting instability of phylogenetic hypotheses about the major clades of Euchelicerata (Giribet and Edgecombe, 2019), it is not unparsimonious to hypothesize that the Acariformes simply retained the plesiomorphic chelicerate condition (Bochkov, 2009; Bolton et al., 2017). The phylogeny in Figure 1 would support epimorphosis as plesiomorphic for the Malacostraca, with secondary independent transition to anamorphosis in some derived taxa, compatible with the presence of a zoea-like larva as the plesiomorphic condition for the group (Jirikowski et al., 2015). However, in consideration of the similarities between the nauplii in anamorphic malacostracans and non-malacostracans and the differences in the direct development of epimorphic malacostracans, other authors have put forward the opposite hypothesis, i.e., the retention of the primitive condition of malacostracan anamorphic larval development in Bathynellacea, Euphausiacea, and Dendrobranchiata and its independent loss in the other malacostracan groups (Akther et al., 2015; Haug and Haug, 2015). Anamophosis and epimorphosis are not fundamentally distinct developmental modes, the latter being only the lower extreme degree of the former. This is more than an arithmetic truism. In several clades, e.g., in decapod crustaceans, segment number is the same in anamorphic and epimorphic lineages. Among the most polymeric epimorphic clade, the Geophilomorpha, Brena and Akam (2013) discovered a minimal leftover of anamorphosis in the species Strigamia maritima, where 2–3 terminal segments (out of 48–54 trunk segments) are added after hatching, during the first embryoid stages (see below). However, the opposite evolutionary transitions, embryonization vs. de-embryonization of segment formation, might not have the same evolvability, the former having apparently occurred more often than the latter. Genetics of Anamorphosis In anamorphic development, as well as in embryonic sequential segmentation, the new segments appear sequentially in anteroposterior progression from a subterminal region referred to as “segment addition zone” (SAZ; Janssen et al., 2010). This is also often referred to as the proliferative (or generative, or growth) zone, but SAZ is to be preferred because it makes no assumption of localized and continuous cell proliferation in the posterior of the body (Clark et al., 2019; see also Fusco, 2005). However, information about morphogenesis and gene expression associated with anamorphosis is scarce, and current investigations are mainly concerned with the evolution of embryonic simultaneous segmentation from embryonic sequential segmentation in insects. Evidence of a conserved role of the segment polarity gene engrailed during anamorphosis was found in the anostracan crustaceans Artemia and Thamnocephalus (Manzanares et al., 1993; Constantinou et al., 2020), in the thecostracan crustacean Sacculina (Gibert et al., 2000) and in the centipede Lithobius (Bortolin et al., 2011). The involvement of Notch signaling is increasingly emerging as a common feature of sequential segmentation throughout the Bilateria. Williams et al. (2012) showed that blocking Notch signaling causes a specific, repeatable effect on segmentation in Artemia franciscana and Thamnocephalus platyurus, although the observation that loss-of-function Notch phenotypes differ significantly across arthropods suggests some variation in the role of Notch in the regulation of sequential segmentation. Despite the paucity of experimental data on the developmental genetics of anamorphosis, some indirect information can be obtained from comparative studies on embryonic segmentation. In a certain way, the evolutionary embryonization of anamorphosis can be seen as a natural experiment, where post-embryonic segmentation, a process not easily accessible to current molecular methodologies, is brought under the eye of the investigator. The extended similarities found in embryonic sequential segmentation in lineages that independently evolved either complete or partial embryonization of segmentation can perhaps indicate a common basic mechanism among lineages with different degree of anamorphosis up to epimorphosis. This could be based on the same clock-and-wavefront mechanism inferred from data on embryonic segmentation in a small number of model species, and hypothesized to be ancestral and conserved among arthropods (Clark et al., 2019). Anamorphosis in Context Beyond the arbitrariness of what to count as the appearance of a new segment, the previous descriptions might suggest that anamorphosis is a well-defined phenomenon, and that its evolution can be confidently traced whenever reliable developmental and phylogenetic information is available. However, this is only a superficial view that can serve only broad comparative purposes. On a closer inspection, seeking for mechanistic explanations, anamorphosis remains surrounded by uncertainties that can be locally resolved only by overcoming the idealizations hidden in the traditional concepts of hatching, larva, and segment. The Blurry Event of Hatching It is not always the case that hatching separates embryonic from post-embryonic phases neatly. More or less embryo-like (embryoid) hatchlings are described for many arthropod groups, under a variety of taxon-specific terms (Minelli et al., 2006; Minelli and Fusco, 2013; Fritsch and Richter, 2015; Haug, 2020; Supplementary Table 1). Focusing on taxonomic distribution and morphological and functional characteristics of these embryoid stages, three facts highlight the evolutionary flexibility of arthropod developmental schedules. First, conditions at hatching are often different between closely related taxa (e.g., in many spiders there is a pronymph with incompletely articulated appendages, but not in all). Second, this diversity is associated with a diversity in the number of molts the animal undergoes before and after the beginning of its active life. In most pterygote insects, three embryonic cuticles are shed before hatching, but only two in the cyclorrhaphous flies (Konopová and Zrzavý, 2005). Third, the condition at hatching is not necessarily correlated to segmentation schedule. For example, epimorphic hexapod hatchlings are anything between an active juvenile and a vermiform pronymph, while anamorphic myriapods hatch in conditions so different as the very active larva I of Lithobius and the motionless pupoid of Pauropus (Minelli et al., 2006). Situated at one extreme of both embryonic and post-embryonic phases, where the methodologies used in the study of each phase are less effective, development around hatching time is little investigated, and recent work is disclosing unsuspected situations. For example, two embryoid stages were traditionally reported for the geophilomorph centipedes, whereas a recent closer scrutiny in Strigamia maritima revealed five stages (Brena, 2014). The Multifaceted Larva Many arthropods, in particular among the Pancrustacea, begin post-embryonic life as larvae. However, the term larva has been applied to immatures with very different, although non-mutually exclusive characteristics. These include forms that differ morphologically from the adult, have different ecological niches than the corresponding adult, or transform into an adult by a metamorphosis (see Haug (2020) for a detailed account), thus the qualification of development as either direct or indirect is somehow a matter of degree or requires qualitative specification (e.g., for some intermediate cases Fritsch et al. (2013) introduced the term pseudo-direct development). The evolution of post-embryonic segmentation, although potentially independent from other developmental features of juvenile stages, can be found to be variably associated to larval evolution, as for instance when the evolution of direct development coincides with a transition to epimorphosis. The Complex Segment Description and comparative analysis of anamorphosis assume that we are dealing with unambiguously countable units, the segments. However, not all putatively segmental structures (especially those of internal anatomy) are in register, as they can have different period or phase. Thus, a more realistic depiction of arthropod body organization is obtained by dissociating the serial homology of individual periodic structures (e.g., legs or sclerites), or segmentation, from the concept of the segment as a body module (e.g., Budd, 2001; Minelli and Fusco, 2004; Fusco, 2005, 2008; Fusco and Minelli, 2013; Hannibal and Patel, 2013). This accounts for the occurrence of so-called “segmental mismatch,” i.e., the discordance between different segmental series within the same animal, and of a number of segmental abnormalities (Leśniewska et al., 2009), but also for the high disparity in arthropod segmental patterns. The study of anamorphosis cannot disregard the complexity and the disparity of the segmentation process (Minelli, 2020). Conclusions We advise that for a better understanding of the developmental changes underlying the evolution of arthropod segmentation, some key concepts should be applied in a critical way. The putative embryonic/post-embryonic divide suffers the same shortcomings shown by the traditional periodization of development (articulation in temporal units for comparative purposes) within each of the two main phases of arthropod development (Minelli et al., 2006). During embryonic development, periodization can either be based on absolute time from egg laying, on the fraction of elapsed embryonic time, or with reference to a series of events such as blastoderm formation, gastrulation, etc. During post-embryonic development, periodization is mainly based on temporal units delimited by molts, generally referred to as stages or instars. In both phases, some developmental events are employed to give temporal order to other events, but there is no biological foundation for one series of events to be recognized as “ordinator” and all other events as “ordered.” Periodization cannot be other than a relative framework, and the same is true for the passage from embryonic to post-embryonic life. Evolutionary developmental biology seems to be over-preoccupied with boundaries, both in space (e.g., those between segments) and time (e.g., those between stages). However, these boundaries can easily hide both the continuity of many co-occurring developmental processes and the independence exhibited to a different degree by the same set of processes (Minelli et al., 2006). As an alternative, for instance, rather than defining embryonic development on the basis of its putative boundaries (fertilization, when the case, and hatching), it seems more sensible to define it based on “what it is,” that is as a special context for early developmental events, characterized by the fact that the latter run protected by the body of a parent (or a host) or by a shell, that are stabilized in physical parameters, occur in relatively small-size living systems, are supplied with energy and materials from the parent, etc. None of these features is necessary, nor sufficient for defining the embryonic phase, and each one can change in evolution with different direction and pace, creating the observed vagueness of the embryonic/post-embryonic divide. From this stance, recurrent embryonization and (although less frequently) de-embryonization of segmentation in evolution reveal the robustness of the developmental processes involved, able to work in contexts so different as an embryo and an active animal, where in many cases these processes can go on for years. Evolution is about change, and to study evolutionary change we need flexible conceptual frameworks and data formats.

Author Contributions Both authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication. Conflict of Interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. Acknowledgments Jason Dunlop, Gregory D. Edgecombe, David A. Legg, Nigel C. Hughes, Jørgen Olesen, and Stefan Richter provided precious help in collecting and checking information on which the article is based. Jørgen Olesen, Stefan Richter, and the two reviewers provided useful comments on an earlier version of the ms.

Supplementary Material The Supplementary Material for this article can be found online at:

References Akther, H., Agersted, M. D., and Olesen, J. (2015). Naupliar and metanaupliar development of Thysanoessa raschii (Malacostraca, Euphausiacea) from Godthåbsfjord, Greenland, with a reinstatement of the ancestral status of the free-living nauplius in malacostracan evolution. PLoS ONE 10:e0141955. doi: 10.1371/journal.pone.0141955 CrossRef Full Text | Google Scholar Bochkov, A. V. (2009). A review of mites of the parvorder Eleutherengona (Acariformes: Prostigmata) – permanent parasites of mammals. Acarina 1, 1–149. Google Scholar Bolton, S. J., Chetverikov, P. E., and Klompen, H. (2017). Morphological support for a clade comprising two vermiform mite lineages: Eriophyoidea (Acariformes) and Nematalycidae (Acariformes). Syst. Appl. Acarol. 22, 1096–1131. doi: 10.11158/saa.22.8.2 CrossRef Full Text | Google Scholar Bortolin, F., Benna, C., and Fusco, G. (2011). Gene expression during post-embryonic segmentation in the centipede Lithobius peregrinus (Chilopoda, Lithobiomorpha). Dev. Genes Evol. 221, 105–111 doi: 10.1007/s00427-011-0359-3 CrossRef Full Text | Google Scholar Brena, C. (2014). The embryoid development of Strigamia maritima and its bearing on post-embryonic segmentation of geophilomorph centipedes. Front. Zool. 11:58. doi: 10.1186/s12983-014-0058-9 CrossRef Full Text | Google Scholar Brenneis, G., and Arango, C. P. (2019). First description of epimorphic development in Antarctic Pallenopsidae (Arthropoda, Pycnogonida) with insights into the evolution of the four-articled sea spider cheliphore. Zool. Lett. 5:4. doi: 10.1186/s40851-018-0118-7 PubMed Abstract | CrossRef Full Text | Google Scholar Brenneis, G., Bogomolova, E. V., Arango, C. P., and Krapp, F. (2017). From egg to no-body: an overview and revision of developmental pathways in the ancient arthropod lineage Pycnogonida. Front. Zool. 14:6. doi: 10.1186/s12983-017-0192-2 PubMed Abstract | CrossRef Full Text | Google Scholar Chipman, A. D., and Edgecombe, G. D. (2019). Developing an integrated understanding of the evolution of arthropod segmentation using fossils and evo-devo. Proc. R. Soc. B 286:20191881. doi: 10.1098/rspb.2019.1881 PubMed Abstract | CrossRef Full Text | Google Scholar Constantinou, S. J., Duan, N., Nagy, L. M., Chipman, A. D., and Williams, T. A. (2020). Elongation during segmentation shows axial variability, low mitotic rates, and synchronized cell cycle domains in the crustacean, Thamnocephalus platyurus. Evodevo 11:1. doi: 10.1186/s13227-020-0147-0 PubMed Abstract | CrossRef Full Text | Google Scholar Enghoff, H., Dohle, W., and Blower, J. G. (1993). Anamorphosis in millipedes (Diplopoda) – the present state of knowledge with some developmental and phylogenetic considerations. Zool. J. Linn. Soc. 109, 103–234. doi: 10.1111/j.1096-3642.1993.tb00305.x CrossRef Full Text | Google Scholar Fernández, R., Edgecombe, G. D., and Giribet, G. (2016). Exploring phylogenetic relationships within Myriapoda and the effects of matrix composition and occupancy on phylogenomic reconstruction. Syst. Biol. 65, 871–889. doi: 10.1093/sysbio/syw041 CrossRef Full Text | Google Scholar Fritsch, M., Bininda-Emonds, O. P., and Richter, S. (2013). Unraveling the origin of Cladocera by identifying heterochrony in the developmental sequences of Branchiopoda. Front. Zool. 10:35. doi: 10.1186/1742-9994-10-35 PubMed Abstract | CrossRef Full Text | Google Scholar Fritsch, M., and Richter, S. (2015). How the cladoceran heterogonic life cycle evolved — insights from gamogenetic reproduction and direct development in Cyclestherida. Evol. Dev. 17, 356–366. doi: 10.1111/ede.12163 PubMed Abstract | CrossRef Full Text | Google Scholar Fu, D., Ortega-Hernández, J., Daley, A. C., Zhang, X., and Shu, D. (2018). Anamorphic development and extended parental care in a 520 million-year-old stem-group euarthropod from China. BMC Evol. Biol. 18:147. doi: 10.1186/s12862-018-1262-6 PubMed Abstract | CrossRef Full Text | Google Scholar Fu, D., Zhang, X., Budd, G. E., Liu, W., and Pand, X. (2014). Ontogeny and dimorphism of Isoxys auritus (Arthropoda) from the Early Cambrian Chengjiang biota, South China. Gondwana Res. 25, 975–982. doi: 10.1016/j.gr.2013.06.007 CrossRef Full Text | Google Scholar Fusco, G. (2008). “Morphological nomenclature, between patterns and processes: segments and segmentation as a paradigmatic case,” in Updating the Linnaean Heritage: Names as Tools for Thinking about Animals and Plants, eds A. Minelli, L. Bonato, and G. Fusco (Auckland: Zootaxa 1950, Magnolia Press), 96–102. doi: 10.11646/zootaxa.1950.1.9 CrossRef Full Text | Google Scholar Fusco, G., and Minelli, A. (2013). “Arthropod segmentation and tagmosis,” in Arthropod Biology and Evolution. Molecules, Development, Morphology, eds A. Minelli, G. Boxshall, and G. Fusco (Berlin Heidelberg: Springer), 197–221. doi: 10.1007/978-3-662-45798-6_9 CrossRef Full Text | Google Scholar Gibert, J.-M., Mouchel-Vielh, E., Quéinnec, E., and Deutsch, J. S. (2000). Barnacle duplicate engrailed genes: divergent expression patterns and evidence for a vestigial abdomen. Evol. Dev. 2, 1–9. doi: 10.1046/j.1525-142x.2000.00059.x PubMed Abstract | CrossRef Full Text | Google Scholar Haug, J. T. (2020). Why the term “larva” is ambiguous, or what makes a larva? Acta Zool. 101, 167–188. doi: 10.1111/azo.12283 CrossRef Full Text | Google Scholar Haug, J. T., and Haug, C. (2015). “Crustacea”: comparative aspects of larval development,” in Evolutionary Developmental Biology of Invertebrates 4: Ecdysozoa II: Crustacea, ed A. Wanninger (Wien: Springer), 1–37. doi: 10.1007/978-3-7091-1853-5_1 CrossRef Full Text Howard, R. J., Puttick, M. N., Edgecombe, G. D., and Lozano-Fernandez, J. (2020). Arachnid monophyly: morphological, palaeontological and molecular support for a single terrestrialization within Chelicerata. Arthropod Struct. Dev. 59:100997. doi: 10.1016/j.asd.2020.100997 PubMed Abstract | CrossRef Full Text | Google Scholar Hughes, N. C., Minelli, A., and Fusco, G. (2006). The ontogeny of trilobite segmentation: a comparative approach. Paleobiology 32, 602–627. doi: 10.1666/06017.1 CrossRef Full Text | Google Scholar Huys, R. (2014). “Copepoda,” in Atlas of Crustacean Larvae, eds J. W. Martin, J. Olesen, and J. T. Høeg (Baltimore: The Johns Hopkins University Press), 144–163. Google Scholar Janssen, R., Le Gouar, M., Pechmann, M., Poulin, F., Bolognesi, R., Schwager, E. E., et al. (2010). Conservation, loss, and redeployment of Wnt ligands in protostomes: implications for understanding the evolution of segment formation. BMC Evol. Biol. 10:374. doi: 10.1186/1471-2148-10-374 PubMed Abstract | CrossRef Full Text | Google Scholar Jirikowski, G. J., Wolff, C., and Richter, S. (2015). Evolution of eumalacostracan development – new insights into loss and reacquisition of larval stages revealed by heterochrony analysis. Evodevo 6:4. doi: 10.1186/2041-9139-6-4 PubMed Abstract | CrossRef Full Text | Google Scholar Koenemann, S., Olesen, J., Alwes, F., Iliffe, T. M., Hoenemann, M., Ungerer, P., et al. (2009). The post-embryonic development of Remipedia (Crustacea)— additional results and new insights. Dev. Genes Evol. 219, 131–145. doi: 10.1007/s00427-009-0273-0 PubMed Abstract | CrossRef Full Text | Google Scholar Leśniewska, M., Bonato, L., Minelli, A., and Fusco, G. (2009). Trunk anomalies in the centipede Stigmatogaster subterranea provide insight into late-embryonic segmentation. Arthropod Struct. Dev. 38, 417–426. doi: 10.1016/j.asd.2009.05.001 PubMed Abstract | CrossRef Full Text | Google Scholar Lindquist, E. E. (1984). “Current theories on the evolution of major groups of Acari and on their relationship with other groups of Arachnida, with consequent implications for their classification,” in Acarology. Proceedings of the 6th International Congress of Acarology, eds D. A. Griffiths and C. E. Bowman (Chichester: Ellis Horwood), 28–62. Google Scholar Manzanares, M., Marco, R., and Garesse, R. (1993). Genomic organization and developmental pattern of expression of the engrailed gene from the brine shrimp Artemia. Development 118, 1209–1219. PubMed Abstract | Google Scholar Minelli, A. (2020). Arthropod segments and segmentation – lessons from myriapods, and open questions. Opusc. Zool. Budapest 51, 7–21. doi: 10.18348/opzool.2020.S2.7 CrossRef Full Text | Google Scholar Minelli, A. (ed). (2015). Treatise on Zoology— Anatomy, Taxonomy, Biology. The Myriapoda, Vol 2. Leiden: Brill. doi: 10.1163/9789004188273 CrossRef Full Text Minelli, A., Brena, C., Deflorian, G., Maruzzo, D., and Fusco, G. (2006). From embryo to adult. Beyond the conventional periodization of arthropod development. Dev. Genes Evol. 216, 373–383. doi: 10.1007/s00427-006-0075-6 PubMed Abstract | CrossRef Full Text | Google Scholar Minelli, A., and Fusco, G. (2013). “Arthropod post-embryonic development,” in Arthropod Biology and Evolution. Molecules, Development, Morphology, eds A. Minelli, G. Boxshall, and G. Fusco (Berlin Heidelberg: Springer), 91–122. doi: 10.1007/978-3-662-45798-6_5 PubMed Abstract | CrossRef Full Text | Google Scholar Miyazawa, H., Ueda, C., Yahata, K., and Zhu, Z.-H. (2014). Molecular phylogeny of Myriapoda provides insights into evolutionary patterns of the mode in post-embryonic development. Sci. Rep. 4:4127. doi: 10.1038/srep04127 PubMed Abstract | CrossRef Full Text | Google Scholar Paterson, J. R., and Edgecombe, G. D. (2006). The Early Cambrian trilobite family Emuellidae Pocock, 1970: systematic position and revision of Australian species. J. Paleontol. 80, 496–513. doi: 10.1666/0022-3360(2006)80[496:TECTFE]2.0.CO;2 CrossRef Full Text | Google Scholar Scholtz, G. (2000). Evolution of the nauplius stage in malacostracan crustaceans. J. Zool. Syst. Evol. Res. 38, 175–187. doi: 10.1046/j.1439-0469.2000.383151.x CrossRef Full Text | Google Scholar Schwentner, M., Richter, S., Rogers, D. C., and Giribet, G. (2018). Tetraconatan phylogeny with special focus on Malacostraca and Branchiopoda: highlighting the strength of taxon-specific matrices in phylogenomics. Proc. R. Soc. B Biol. Sci. 285:20181524. doi: 10.1098/rspb.2018.1524 PubMed Abstract | CrossRef Full Text | Google Scholar Williams, T., Blachuta, B., Hegna, T. A., and Nagy, L. M. (2012). Decoupling elongation and segmentation: Notch involvement in anostracan crustacean segmentation. Evol. Dev. 14, 372–382. doi: 10.1111/j.1525-142X.2012.00555.x PubMed Abstract | CrossRef Full Text | Google Scholar

Complete metamorphosis (fly) Most arthropods lay eggs, but there are a few that produce live young. One of the disadvantages of having an external skeleton is that growth cannot proceed gradually, and so during their life arthropods have to moult a number of times, becoming a little larger each time. Among the insects, development is associated with the process known as metamorphosis, which can take place in two different ways. In some insects, such as bed bugs and cockroaches, the newly hatched young look like miniature versions of the adults. They go through a number of stages, separated by a series of moults. This is known as incomplete metamorphosis. Incomplete metamorphosis (bed bug) Other insects, such as flies, beetles and butterflies, have complete metamorphosis, in which the young stages show no resemblance at all to the adults. Here a special immobile stage, the pupa, occurs between the larva and the adult. When the adult insect emerges from the pupal stage it ceases to grow, so there is no truth in the idea that, for example, small flies can become large flies. Biologist at Statens SkadedyrslaboratoriumAuthor of:"Pests in House and Home""Bed Bugs - Bites, Stings and Itches""Food Pests""Husets dyreliv" (Insects Around the House - Only danish)"Skadedyr i træ" (Timber Pests - Only danish)"Stuefluen" (Common Housefly - Only danish) Latest posts by Henri Mourier (see all) Article Open access 15 March 2023 Article Open access 25 January 2022 Developmentally, arthropods proceed from an egg, through larval and/or nymphal stages, to the adult. Generally, the term "larva" applies to stages in which major morphological changes occur, and these stages are often fixed in number. The term "nymph" is applied to stages which change in little other than size between molts, and are usually indeterminate in number. Of course, given the diversity of the arthropods, there has developed a diversity of nomenclature for the different larval or nymphal stages that rivals that of the Platyhelminthes. Arthropods are usually ectoparasites, and may require 1 or more hosts to complete their life cycle. Many species move freely from one host to another, but others become attached permanently. Some species complete the entire life cycle on the host, but others attach only to feed and mate. Aquatic hosts usually harbor crustacean parasites, whereas terrestrial hosts harbor insects and arachnids.

. 2025 Apr 16;292(2045):20242950. doi: 10.1098/rspb.2024.2950

The segmented body is a hallmark of the arthropod body plan. Morphological segments are formed during embryogenesis, through a complex procedure involving the activation of a series of gene regulatory networks. The segments of the arthropod body are organized into functional units known as tagmata, and these tagmata are different among the arthropod classes (e.g. head, thorax and abdomen in insects). Based on embryological work on segment generation in a number of arthropod species, coupled with a survey of classical descriptions of arthropod development, I suggest a new framework for the evolution of arthropod tagmata. The ancestral condition involves three developmental tagmata: the pre-gnathal segments, a tagma that is formed within a pre-existing developmental field and a tagma that is formed through the activity of a segment-addition zone that may be embryonic or post-embryonic. These embryonic tagmata may fuse post-embryonically to generate more complex adult tagmata. This framework is consistent with the evolution of tagmosis seen in the early arthropod fossil record. It also calls for a re-thinking of the decades-old division of arthropod development into short-germ versus long-germ development, a re-thinking of questions of segment identity determination and the role of Hox genes in tagma differentiation.

Keywords: arthropods, tagma, segment identity, Hox genes, body plan

The arthropod body plan is characterized by repeated morphological units, or segments, along the antero–posterior axis. These segments are usually organized into higher level units, each composed of several segments, known as tagmata (tagma in singular). The segments of each tagma normally have shared functions, and roughly similar size and shape, and they are often differentiated from the segments of the adjoining tagmata by a distinct morphological boundary. While the nature and composition of the tagmata vary among arthropod classes, they are more or less conserved at the level of the class, and are often used as defining characters of the class. The term ‘tagma’ itself is used relatively loosely in the literature, corresponding to the inherent variability in tagmata. The morphological literature has given a lot of attention to the defining features of different tagmata, and to the variability in their composition, but there has been almost no recent discussion of the evolutionary history of the tagmata or of their development. I present a synthesis of what is known about tagmosis (the arrangement of segments into tagmata) from comparative morphology, from developmental biology and from the fossil record. I use this synthesis to suggest a novel model for the evolution of arthropod tagmata. I argue that conserved elements of developmental tagmosis form the basis for much of the observable tagmata. The details of arthropod tagmosis have been extensively reviewed by Fusco & Minelli [1], and will not be repeated here. I will give a brief overview of the typical tagmosis pattern in the main arthropod lineages, emphasizing the most likely plesiomorphic condition for each lineage. The basic chelicerate body plan is composed of two tagmata, usually known as the prosoma (or cephalothorax) and opisthosoma (or abdomen). This is most clearly seen in the terrestrial arachnids, exemplified by spiders. The prosoma includes four pairs of walking appendages and anterior to them two pairs of feeding or sensory appendages, the pedipalps and the chelicerae. The anterior-most segment of the prosoma carries the eyes and the labrum. The opisthosoma normally does not carry walking appendages, but may carry breathing appendages, or specialized structures such as spinnerets. There are numerous minor variations on this theme, and these have been reviewed extensively by Dunlop & Lamsdell [2]. In pycnogonids, the number of walking appendages can vary, and the opisthosoma is rudimentary or nonexistent [3]. Some arachnids have a subdivided opisthosoma (e.g. scorpions), whereas in others there is no clear border between the prosoma and opisthosoma (e.g. acarids, opiliones). Nonetheless, it is generally accepted that the two-tagma structure is ancestral to extant chelicerates, as are four pairs of walking appendages and two sensory/feeding appendage pairs in the prosoma [2]. The myriapod body plan consists of a head and a mostly homonomous trunk. The head is composed of six segments: three pre-gnathal segments and three gnathal segments. This is the composition of the head in all members of Mandibulata (Myriapoda + Pancrustacea). The pre-gnathal segments include the three parts of the brain and carry eyes on the first segment and a pair of antennae on the third segment. The gnathal segments carry feeding appendages [4]. The trunk is composed of all of the remaining segments, most of which carry a pair of walking appendages. The myriapod trunk may display a number of lineage specific novelties, such as a mid-body transition zone in many centipedes, or a mismatch between dorsal and ventral segmentation in millipedes. There may be specialized segments, such as the centipede venom-claw or the posterior-most segment, or gonopods used for sperm transfer in millipedes. In some cases, there is some degree of regionalization within the trunk [4]. Nonetheless, none of these specializations alters the basic tagmosis of the myriapod body plan, which is always composed of a head and a trunk. The non-hexapod pancrustaceans display a bewildering array of tagmosis patterns [5]. In all cases, the anterior-most tagma is a six-segment mandibulate head, although the head is not always separated by a clear morphological boundary from the tagma behind it. Indeed, the head is often covered by a head shield or carapace that also covers segments posterior to the head. The region covered by the carapace is sometimes known as a cephalothorax, although this is a very different structure from the one known by the same name in chelicerates. The trunk of malacostracan crustaceans is usually divided into two regions, known as a pereon and pleon. The pereon carries walking appendages, as well as maxillipedes, which are modified appendages used in feeding. The pleon usually does not have walking appendages, but often has other modified appendages. In brachyurans, as well as in other ‘crab-like’ crustaceans, most or all of the pleon is reduced and folded ventrally under the pereon [5,6]. Insects and their close relatives in Hexapoda have the most consistent pattern of tagmosis among arthropods. The body is composed of three sharply defined tagmata: a six-segment mandibulate head, a three-segment thorax with walking appendages and an abdomen with usually between 9 and 11 segments or as few as 6 in Collembola, which normally does not carry appendages [7]. There are minor variations on this structure. For example, in some hymenopterans, the border between the thorax and the abdomen shifts. The head and thorax are sometimes fused, as in some psyllids. In some holometabolous insects, there is a reduction in the number of adult abdominal segments. Nonetheless, there is little doubt that the ancestral pattern of tagmosis is the common three-tagma structure. The earliest arthropod stem-group members, the paraphyletic assemblage known as lobopodians, show no tagmosis, and are thus similar to the extant arthropod sister groups, onychophorans and tardigrades [8]. The head is composed of a single segment, with no additional segments attached to it [9]. While there may be some regionalization and specialization of specific segments along the trunk, these are not grouped into functional regions and do not display morphological borders, and should thus not be considered as tagmata. The gilled lobopodians (such as Kerygmachela and Pambdelurion), as well as diverse organisms as Opabinia and the radiodonts, also have a single-segment head, and no obvious tagmata within the trunk. The single head carries the eyes and usually a single pair of large raptorial or sensory appendages [10,11]. Members of these groups display varying degrees of regionalization. The size of the segments and appendages varies along the body axis, but without a sharp discontinuity. The neck region in radiodonts is a distinct group of 4−5 segments, but it is not delimited by a morphological boundary. The tail fan is a distinct structure in some gilled lobopodians and radiodonts, and it may be composed of a number of segments [12,13]. All this considered, while members of the gilled lobopodian/radiodont grade start to show increasing levels of regionalization, there are no obviously differentiated tagmata. Deuteropoda is the clade that includes both crown-group arthropods and the upper stem group. Members of Deuteropoda have three pre-gnathal segments [14]. In the upper stem group, these three segments comprise the entire head (but see O’Flynn et al. [15] for a different viewpoint). These head segments often bear specialized appendages (sometimes called ‘great appendages’). In some cases, there are 1−3 specialized appendages just posterior to the head [16–19]. It is possible to describe these animals as having a distinct head and trunk, as in myriapods, although the head is composed of only three segments. It is not clear whether the specialized post-cephalic appendages should be considered part of an expanded head, as in extant mandibulates, or modified trunk segments, since there is no sharp morphological boundary. These appendages may be the precursors of the gnathal segments in mandibulate arthropods. Tagmosis in trilobites and its development have been studied fairly extensively due to the excellent fossil record of these animals, which allows the reconstruction of complete post-embryonic developmental series, most notably in Aulacopleura konincki [20,21]. The trilobite body is divided into three tagmata: the cephalon (or head), thorax and pygidium. The posterior border of the cephalon is clear and stable and is established in the earliest recoverable stages, which have a head only, or a head with a single additional segment. However, the thorax and pygidium are dynamic, with new segments being added to the pygidium in successive moults, and then ‘released’ to the thorax, to maintain a more-or-less stable number of pygidial segments, and a growing number of thoracic segments [22]. The thorax–pygidium border is thus a dynamic border, and the tagmata themselves vary in number of segments and in the border between them throughout ontogeny. In this sense, they are unlike the tagmata in all extant arthropods and in most fossil arthropods. Stem-group chelicerates all have a distinction between a prosoma and an opisthosoma, but the number of segments in each of these tagmata and the identity of the appendages carried on these segments do not always conform to what is found in extant chelicerates. The diversity and evolution of tagmata in fossil chelicerate taxa were also discussed in the review by Dunlop & Lamsdell [2]. Stem-group mandibulates have a typical head tagma and variable posterior tagmata. Their diversity has been reviewed by Waloszek & Maas [23]. A more recent alternative framework for the mandibulate stem group is outlined by Izquierdo-López & Caron [24]. They reconstruct only two segments posterior to the pre-gnathal segments, rather than the three found in extant mandibulates. The basis for tagma differentiation is laid down during embryonic development. While this statement sounds intuitively almost obvious, the embryonic basis of tagmosis has hardly been studied, and has only been looked at explicitly in a handful of species. There is, however, enough implicit information in both classical and modern descriptions of embryonic development to be able to draw some general conclusions. I argue that embryonic regionalization of segments forms a more conserved and ancient tagmosis than the apparent tagmosis seen in the adult body plan. The connection between regionalization of embryonic segments and adult tagmata is not direct, and there is often a mismatch between the two. The most obvious example is in the PGS. There is an ongoing debate about the evolutionary origin of these units [25,26], with Lev & Chipman [27] arguing that they should not even be considered segments. However, regardless of these differing opinions, there is no doubt that the three anterior segments in all arthropods develop differently and stand on their own as a distinct embryonic unit, despite being incorporated into the adult head (in mandibulates) or prosoma (in chelicerates). In mandibulates, the three posterior segments of the head, the gnathal segments, are indistinguishable from the segments immediately posterior to them during the early stages of development. In most insects, the gnathal and thoracic segments (abbreviated as gnatho-thoracic segments hereafter) form a distinct series of six segments that form together and are of similar size and shape, until the differentiation of the appendages (mouthparts or walking legs) [28–31]. In myriapods, the gnathal segments are identical to trunk segments in the early germ-band before appendage differentiation [32,33]. In chelicerates, prosomal segments and opisthosomal segments have different morphologies [34–36], although this is probably mostly due to the presence of walking limbs on prosomal segments, which affect the segments’ morphology. In many cases, there are also differences in the way different segments are formed. In what follows, I review what is known about these differences in species where all segments are formed during embryogenesis (epimorphic development). Species where some of the segments are formed post-embryonically (anamorphic development) are discussed in §4. The similarity between gnathal and thoracic segments is not limited to their morphology in the germ-band stage. In many cases, they also develop through a similar developmental programme. This similarity has been best demonstrated in the milkweed bug Oncopeltus fasciatus (figure 1a). In this species (and in other hemipterans), early development can be divided into a blastoderm stage and a germ-band stage [37–39]. In the blastoderm stage, the embryo is composed of a single layer of cells covering an ovoid yolk mass. The cells of the blastoderm then undergo a process of invagination, to form a germ-band that is embedded inside the yolk. The segmentation process begins already in the blastoderm stage, with orthologues of the Drosophila segmentation cascade genes being expressed in sequence to form segmental stripes of segment polarity genes such as engrailed and wingless [40]. During this early phase of segmentation, the gnatho-thoracic segments are patterned at the molecular level, and the borders between them are established by the interactions of the segment-polarity network. There is no morphological evidence of segmental borders during the blastoderm stage. Schematic representation of the different modes of segment generation in four insect species. (a) In the milkweed bug Oncopeltus fasciatus, two of the pre-gnathal segments (red) and the gnatho-thoracic segments (green) are patterned nearly simultaneously in the blastoderm. Germ-band condensation (marked with a black arrowhead) occurs through a process of invagination. The abdominal segments (blue) are patterned sequentially in the germ band. The third pre-gnathal segment, the intercalary segment, is patterned during abdominal segmentation, as in many insects. (b) In the German cockroach Blattella germanica, there is no sharp distinction between a blastoderm and germ-band stage. However, the gnatho-thoracic segments are patterned rapidly and sequentially in a pre-patterned field, which then condenses to form the germ-band, where abdominal segmentation takes place. (c) In the well-studied fruit fly, Drosophila melanogaster, all segments are patterned simultaneously in the blastoderm, followed rapidly by the condensation of the germ-band. (d) In the flour beetle Tribolium castaneum, all segments are patterned sequentially. However, there is a difference in rate between the gnatho-thoracic segments and the abdominal segments, and the segment-addition zone is only active during abdominal segmentation. Germ-band condensation occurs simultaneously with gnatho-thoracic segmentation (marked with a broad black arrowhead).During the invagination process, the embryonic tissues condense to give the germ-band, and shortly afterwards, the gnatho-thoracic segments can be seen morphologically [41]. About halfway through the invagination process, a specialized embryonic zone forms at the posterior of the germ band, and it is from this posterior zone, known as the segment addition zone (SAZ) or growth zone, that the abdominal segments start appearing sequentially [42]. The question arises whether this distinction between gnatho-thoracic and abdominal segmentation is unique to hemipterans, or whether a similar distinction can be seen in the development of other insects. An analysis of an additional species of hemimetabolous insects, together with a survey of reported segmentation patterns in other insects, suggests that this may be a general pattern—at least in hemimetabolous insects—although the details may vary. In the German cockroach Blattella germanica (figure 1a), the gnathal and thoracic segments are patterned sequentially at the level of segment polarity genes, but the pair rule gene even-skipped is expressed more or less simultaneously in all gnatho-thoracic segments, and fades sequentially, with hedgehog expression coming up in its place. Only after all of the gnatho-thoracic hedgehog expression stripes come up, does the SAZ form and abdominal segments appear sequentially, driven by a cyclic expression of even-skipped [31]. In the cricket Gryllus bimaculatus, gnatho-thoracic stripes of hedgehog expression come up rapidly and sequentially. There is then a gap of a few hours before the SAZ forms and abdominal segments arise sequentially [43]. This pattern is similar to that seen in B. germanica. A closer analysis of the pattern in these three hemimetabolous insects shows that the main difference between the formation of gnatho-thoracic and abdominal segments is not whether they are formed simultaneously or sequentially. The main difference is in the embryonic environment in which they are formed. Gnatho-thoracic segments are patterned within a pre-existing embryonic field or anlage, whereas abdominal segments are formed from a posterior domain where axial elongation is taking place—the SAZ. Detailed descriptions of segmentation in additional hemimetabolous insects are rare, but a survey of the literature suggests a similar pattern in many cases (see electronic supplementary material, table S1 for examples). Anterior segments form within a pre-existing field, without addition of new tissue, and posterior segments form from an SAZ. The border between the two processes is not always evident from the existing description, but the data are consistent with the border being the thoracic-abdominal border. Even in short-germ insects such as the grasshopper Schistocerca, the early embryonic field encompasses only the gnathal segments and expands through tissue condensation to include the thoracic segments [28]. Only after this process is done are abdominal segments added sequentially. Since hemimetabolous insects form a paraphyletic group, basal to the more widely studied Holometabola, we can assume that the pattern described above is the ancestral segmentation mode for insects. This pattern was thus presumably lost in Holometabola, otherwise, it would have been discovered before, given the extensive body of work on holometabolan development (e.g. Drosophila melanogaster; figure 1c). But is this really the case? In the well-studied red flour beetle Tribolium castaneum (figure 1d), a study of the dynamics of segment generation showed that the thoracic segments form at a uniform rate, there is then a slowing down of the process, followed by a dramatic increase in segmentation rate during abdominal segmentation [44]. Indeed, looking at the germ band of T. castaneum, the SAZ is only evident during abdominal segmentation, with gnatho-thoracic segments being patterned in a rapidly condensing—but not extending—embryonic field. In the parasitic jewel wasp Nasonia vitripennis, where there is no obvious SAZ, there is a transition in segment generation between the six anterior segments (the gnatho-thoracic segments) and the posterior abdominal segments [45]. The first three pair-rule stripes (corresponding to the six anterior segments) arise simultaneously and the following stripes arise in what has been called ‘progressive segmentation’—e.g. sequential segmentation without an SAZ [46]. Even in Drosophila melanogaster, the paradigm for simultaneous, long-germ segmentation, there are two patterning centres: an anterior patterning centre responsible for gnathal and thoracic segments, and a posterior centre responsible for abdominal segments [47–49]. Even when all obvious evidence of a difference in segmentation mode between segments has been lost, there is a vestige hinting at an ancestral distinction between two groups of segments. The diverse morphologies and tagmosis modes seen in crustaceans are reflected in diverse modes of segmentation. There is not a lot of information about embryonic segmentation in different crustaceans. Most crustaceans for which we have any information display indirect development, hatching as a larva with only three visible segments—two pairs of antennal segments and the mandibular segment. This type of larva is known as a nauplius [50], and is discussed in §4 on post-embryonic segmentation. Species with direct development are found throughout crustacean diversity. In many cases, even when all segments are formed during embryogenesis, there is an early developmental stage where the three naupliar segments develop and start differentiating, before the appearance of any other segments. This stage is called the ‘egg nauplius’, and is usually understood to be homologous to the recently hatched nauplius of indirect developing species [51,52]. An example of such development can be seen in the branchiopod Daphnia magna [53,54]. In this species, the naupliar segments appear very early in development, followed by all posterior segments. However, the posterior segments do not follow a strict anterior–posterior sequence. The two maxillary segments, which will form part of the adult head, appear at a slight delay relative to the thoracic segments, suggesting the possibility of a somewhat different mechanism underlying their formation, relative to the sequential, SAZ-based formation of thoracic segments. The crustacean group in which embryonic development has been best studied is Malacostraca. Most malacostracan crustaceans form their segments through posterior stem cells known as ectoteloblasts [55,56]. In this mode of segmentation, every division of the ectoteloblasts generates a daughter cell that will be the precursor to cells of a single parasegment. Segmentation via ectoteloblasts has been studied in the isopod Porcellio scaber (among others) [57–59]. The anterior segments, including the pre-gnathal and gnathal segments, are formed through cell rearrangements prior to the activity of the ectoteloblasts. All segments from the first thoracic segment onwards are formed sequentially via divisions of the ectoteloblast row. It is worth noting that in post-hatching morphology, the cephalothorax, which is the anterior-most tagma, includes the pre-gnathal and gnathal segments, in addition to the first thoracic segment. Studying the neural development of two crayfish species (members of Malacostraca), Vilpoux et al. [60] showed that the central nervous system in the naupliar region (pre-gnathal + mandibular neuromeres) develops almost simultaneously. After its formation, there is a short lag, after which the posterior neuromeres develop sequentially. The best studied model for crustacean embryonic segmentation is the amphipod Parhyale hawaiensis. However, similar to D. melanogaster, and in common with all amphipods, P. hawaiensis displays a simultaneous mode of segment generation, which is almost certainly derived [61,62]. In all amphipods, ectodermal cells assemble into a grid, without going through the sequential ectoteloblast divisions typical of other malacostracans. The pre-gnathal and mandibular segments (the naupliar segments) display a slightly different mode of assembly, whereas there is no noticeable difference in the way all other segments are formed. In the centipede Strigamia maritima (figure 2a), a ‘head bulge’ appears from the germ disc before segmentation begins, and the PGS form within this bulge [33]. The gnathal segments, the segment bearing the venom-claw and the first leg-bearing segment appear nearly simultaneously [32,33,63]. All posterior segments form sequentially, initially with a two-segment periodicity of a segmentation clock [64]. There is no apparent difference in the segmentation of the gnathal and trunk segments. Towards the end of the segmentation process, there is a shift from a pattern where two segments are patterned from each stripe of even-skipped expression to one where each even-skipped stripe generates a single segment [65]. Schematic representation of the different modes of segmentation in four arthropod species. (a) In geophilomorph centipedes (such as Strigamia maritima), the germ band condenses (black arrowhead) during the segmentation of the pre-gnathal segments (red) and the gnathal segments (green), without the activity of a segment addition zone. Trunk segments (blue) are formed mostly two at a time (transparent fill and dotted lines indicate that not all segments are portrayed). Segmentation ends well before hatching (white arrowhead). (b) In scutigeromorph centipedes, anterior segmentation is probably similar to that of geophilomorph centipedes, although there is very little data). Four trunk segments form during embryogenesis, with successive segments added post-hatching. (c) In arachnids, including spiders and others, the pre-gnathal segments and the limb-bearing segments are patterned rapidly within the early embryonic disc. The disc then condenses to give the germ-band, and opisthosomal segments are patterned sequentially from a segment-addition zone. (d) In crustaceans that have a nauplius stage, the pre-gnathal segments and the mandibular segments are patterned embryonically. The germ-band condenses and the nauplius hatches, with additional segments added sequentially. In crustaceans without a nauplius stage (not shown), the main difference is that hatching is heterochronically shifted to after the end of segmentation.The only diplopod species where segmentation has been studied is the pill millipede Glomeris marginata [66]. Segmentation in this species is not very different from that of the centipede S. maritima. Segmentation is sequential throughout, with the first few segments appearing more or less simultaneously, with no obvious difference between gnathal segments and trunk segments. Typically for diplopods, there is a mismatch between dorsal and ventral segmental patterning, with each dorsal tergite corresponding to two ventral leg-bearing segments. This mismatch is only seen in the trunk segments, and not in the head segments, where dorsal and ventral segments are aligned. The anterior-most trunk segment also shows no dorsoventral mismatch [66]. In spider segmentation, the prosomal segments are patterned rapidly within the initial germ disc, without any extension of the disc (figure 2c). After prosomal segments are formed, the SAZ begins to function, generating single segments sequentially through a cyclic process [35,67–69]. This pattern is seen both in the wandering spider Cupiennius salei and in the house spider Parasteatoda tepidariorum. A similar pattern is seen in other arachnids where segmentation has been studied, although the details are usually not as clear. Both in the whip scorpion Phrynus marginemacultus [70] and in the harvestman Phalangium opilio [71], the prosomal segments are formed rapidly within the germ disc, while the opisthosomal segments are formed sequentially from an SAZ. There are two main modes of post-embryonic (or anamorphic) segmentation found within arthropods. The first is addition of segments within a nauplius/post-nauplius larva (figure 2d). In this mode, segment addition takes place in a free-swimming larva that hatches with a minimal number of segments. Segment addition is not normally accompanied by moulting. Although there are moults during the segment addition process, they are few relative to the number of segments added. The process occurs continuously and at a relatively constant rate [72]. This mode of post-embryonic segmentation is found in some crustacean taxa and may be ancestral to Pancrustacea. The second mode is the addition of segments in sequential moults, in an animal that hatches with functional walking limbs. This is the case in a number of myriapod taxa and in some crustaceans, and it is also found to a limited extent (addition of a single post-embryonic segment) in some mites and in oniscidian isopods. Post-naupliar segment addition has been studied in only a handful of crustacean species [72–74]. In all cases, the two antennal segments and the mandibular segment form rapidly in embryogenesis. The development of the ocular segment, which lies anterior to the antennal segments, is usually not described explicitly, but it is probably determined early in larval development. The post-mandibular segments arise sequentially, and there is no apparent difference in their mode or dynamics of development. In the fairy shrimp Thamnocephalus platyurus, the thoracic and abdominal segments are different in shape and size, but arise similarly [72]. Centipedes of the orders Scutigeromorpha (figure 2b) and Lithobiomorpha hatch from the egg with four or six to eight leg-bearing segments, respectively. Additional segments are added one or two at a time in successive moults, up to a total of 15 leg-bearing segments [4]. Most millipedes also hatch with seven leg-bearing segments and add segments in successive moults, with no clear final number of segments [4]. The development of the pycnogonids (sea spiders) is very diverse, but the most common mode of development involves the hatching of a pronymphon larva that includes the pre-gnathal segments (hereafter PGS) and an additional one or two segments, similar to the situation in crustaceans with a nauplius. Additional segments are added in successive moults [75]. The arthropod fossil record indicates that post-embryonic segment addition was much more phylogenetically diverse in the past. A number of fossil taxa have a rich enough fossil record that allows reconstruction of post-embryonic developmental series. This has already been discussed above for trilobites, and it is important to point out here that the earliest developmental stage found for trilobites is a head larva, with no externally obvious segmentation. It is not clear how many segments these larvae contain, but based on exceptionally preserved fossils of adult trilobite heads, they probably contain five segments, presumably including the PGS and two additional cephalic appendages [76]. ‘Orsten’-type fossilization is an exceptional mode of preservation wherein small individuals are fossilized in exquisite detail through phosphatic replacement of organic tissues. Late Cambrian Orsten fossils provide a wealth of information about larval development in crustaceans and their relatives. These fossils indicate that the nauplius is a very early invention within the crustacean lineage, and that sequential post-naupliar segment addition was established and common by the late Cambrian [77,78]. Developmental series for a number of stem and putative crown group arthropods have been published in the past decade. These include the radiodont Stanleycaris [79,80], the upper stem arthropods Isoxys [81] and Chandianella [82], and the putative crown arthropods Leanchoilia [83,84] and Fuxianhuia [85]. All of these cases indicate that post-embryonic segment addition was found throughout arthropod phylogeny in the early stages of their evolution. However, none of these developmental series is as complete as that of trilobites, so we do not know the minimal number of segments with which these animals hatched from the egg. The many different patterns of tagmosis found in extant arthropods emerged from an unknown ancestral pattern. I suggest that ancestral tagmosis was originally a developmental phenomenon, with the segments of diverse regions of the animal patterned differently. Over evolutionary time, the segments that were patterned using different developmental mechanisms evolved differential morphologies and different functional roles. The original differences in development are preserved to varying extents in extant arthropods. In many cases, the borders between regions that are patterned differently are preserved as tagma borders. In some cases, the mode of development has changed so the developmental borders are not immediately obvious. In many cases, additional tagmata evolved as sub-divisions of the original ones. In other cases, there has been fusion within and between adult tagmata, masking the original borders, although these can still be seen in development (figure 3). A schematic tree of the main panarthropod groups mentioned in the text, with the major evolutionary events related to tagmosis mapped on the tree. The tips are extant genera for which there exist developmental data. Genera listed vertically represent fossil species for which we have ontogenetic data. (a) In the common ancestor of Panarthropoda, there was a single-segment head and an undifferentiated trunk region. (b) Post-embryonic segment addition appeared in stem-group arthropods. This may also represent the first appearance of a segment addition zone. (c) Deuteropoda is characterized by the appearance of the three-segment head, representing a novel developmental tagma with a unique mode of segment generation: the pre-gnathal region. (d) The common ancestor of Arthropoda already had three distinct developmental tagmata: the pre-gnathal segments, a tagma including segments developing in a pre-existing field, and a tagma with segments generated from a segment addition zone. (e) Trilobites have a unique mode of tagmosis, involving segment release between the pygidium and the thorax. (f) All extant arachnids have a prosoma composed of the pre-gnathal segments and an embryonic tagma with four segments formed in a pre-existing field, and an opisthosoma, with a variable number of segments formed from a segment addition zone. In stem arachnids, the number of segments formed in each tagma varies, but the general arrangement is the same as in extant arachnids. (g) In myriapods, the number of segments formed within a pre-existing field is three or four, including the gnathal segments and possibly one post-gnathal segment. (h) The nauplius appeared early in the evolution of Pancrustacea, although it is not clear if it is a synapomorphy of the entire clade. All pancrustaceans have a pre-gnathal region and a tagma including segments generated from a growth zone. The number of segments developing within a pre-existing field is variable and may be as low as a single segment in some lineages. (i) In Malacostraca, the segment addition zone functions via specialized stem cells: ectoteloblasts. (j) In insects, the thorax, a novel tagma, first appears. It is composed of three of the segments formed within a pre-existing field, with an additional three segments, the gnathal segments, fusing with the head as in other mandibulates. (k) In Holometabola, the developmental distinction between gnatho-thoracic segments and abdominal segments is masked, with the evolution of novel segmentation modes.In the common ancestor of all arthropods, segments were patterned via three mechanisms: (i) the anterior three segments (the PGS) were patterned separately and not always in sequence with other segments, via a developmental mechanism that did not involve pair-rule gene homologues, and probably including a mechanism of ‘stripe-splitting’; (ii) a number of trunk segments, probably numbering on the order of 5−10 segments, were patterned within a pre-existing embryonic field, either by subdivision of the field (simultaneous segmentation) or through a sequential process that did not involve the addition of new embryonic tissue (progressive segmentation); and (iii) posterior segments were patterned sequentially, through the activity of a segment addition zone (growth zone), which involved axis extension via a combination of the generation of new tissue through cell division and of convergent extension movements of the SAZ. Vestiges of these three segmentation mechanisms can be found in almost all extant arthropods. I raise the intriguing possibility that originally, the distinction between the second segmentation mechanism (segmentation within a pre-existing developmental field) and the third mechanism (segmentation from an SAZ), was a distinction between embryonic and post-embryonic segmentation. In a previous paper [86], I made the implicit assumption that the common ancestor of all arthropods was a direct developer forming all segments during embryogenesis, and that indirect development evolved convergently in different lineages. This was based mostly on lack of evidence for indirect development in the fossil record. Subsequently, Wolfe [87] argued that metamorphosis was ancestral, based on phylogenetic considerations. With the new data available, I suggest a revised and intermediate solution. The last arthropod common ancestor was hemianamorphic (i.e. some segments were formed in embryogenesis and some post-embryonically). The anamorphically forming segments were generated via an SAZ in a gradual process, with new segments probably appearing during the moulting process. Indeed, the SAZ may have evolved as a developmental mechanism for post-embryonic segment generation. Since the closest sister groups to arthropods (onychophorans and tardigrades) both generate all segments during embryonic development, we cannot say for certain when post-embryonic segmentation, and by extension the SAZ, evolved. However, the fact that we find post-embryonic segment addition in a radiodont provides a possible phylogenetic bracketing [80]. The extent of the segments formed in a pre-existing field (hereafter PEF segments) varies in different arthropods. This field still exists as a clear and distinct field in arachnids and in insects. In insects, it comprises six segments (gnathal + thoracic). In arachnids, it comprises four segments (walking limbs). In crustaceans with a nauplius larva, it may have been lost, with only one post-PGS segment (the mandibular segment) patterned not via the SAZ. Nonetheless, in some crustaceans, the first few post-naupliar segments appear simultaneously, which may be a vestige of this mechanism. In myriapods, the pre-existing field is not as distinct, but the dynamics of segmentation suggests that the SAZ only starts generating segments from the first or second trunk segment, indicating that at least the embryonic gnathal segments are within this field. Most of the diversity of developmental tagmosis modes in different arthropods can be seen as stemming from variation in three parameters: (i) the number of segments patterned under each of the mechanisms, (ii) the point in development at which the germ band condenses and gastrulation takes place, and (iii) the stage of development at which the embryo hatches. The latter two are based on heterochronic shifts, which can occur fairly rapidly and easily from an evolutionary point of view. The former tends to be conserved at high taxonomic levels, although departures from the taxon-typical mode can be found. The diversity of arthropods is such that there are many examples of unusual development and tagmosis. The strangeness of these examples should not distract us from identifying the deeply rooted ancestral pattern. For nearly a century, the literature on insect and arthropod development has made the distinction between short-germ development and long-germ development [88–90]. The difference lies in the extent of the embryo that is patterned before gastrulation, or germ-band condensation. In long-germ development, the entire embryonic axis is patterned prior to gastrulation, and in short-germ development only a small part of the axis is (usually only the head). Intermediate-germ is used for cases where the head and thorax are patterned prior to gastrulation. Short- and long-germ development are often also used to make a distinction between simultaneous and sequential segmentation, although this was not the original meaning of the terms. The proposed model for the evolution and development of tagmata requires a reframing of long- and short-germ development in the context of the different embryonic tagmata. Two separate modes of segmentation exist in almost all arthropods, except for in the most extreme cases of long-germ simultaneous segmentation such as Drosophila. The main difference between the modes is in the heterochronic shift of gastrulation and germ-band condensation relative to the segmentation process. The head of mandibulate arthropods (myriapods, crustaceans and insects) incorporates segments from two embryonic tagmata: the PGS and the PEF segments [91,92]. The fossil record shows that the ancestral head in crown group arthropods was composed of only the PGS [26]. The evolution of the mandibulate head initially involved the fusion of the entire PEF tagma with the PGS to give rise to the six-segment head (although stem mandibulate fossils suggest this may have originally been only two PEF segments and a five-segmented head [24]). This is the case in extant myriapods and may be the ancestral mode in crustaceans (but see discussion of head larvae in §6d). Insects are the largest class within arthropods and the most conservative in terms of their overall body plan (despite being extremely variable in modifications of this body plan). Perhaps one of the sources of the insects’ success is the tightly integrated thorax, which specializes in locomotory function, and has no direct equivalent in any other arthropods class. The uniqueness of the insect thorax extends to its developmental origin. There is no other case where the PEF tagma subdivides into two functional adult tagmata. In myriapods and in non-hexapod crustaceans, the PEF is small—probably only three segments—and is entirely incorporated into the mandibulate head. In insects, this tagma encompasses six segments, half of which are incorporated into the head and half of which form the thorax. This realization puts the evolution of the insect body plan in a new light and suggests additional avenues for evo-devo research, while also predicting potential transitional body plans that might be found in the fossil record. The term ‘head larva’ is often used to describe larval forms that comprise only 3−4 segments, essentially the PGS and possibly an additional gnathal segment. The best-known head larvae are the nauplius larvae common in many crustaceans (and possibly plesiomorphic for Pancrustacea), but head larvae are also found in some pycnogonids and in horseshoe crabs. Because of their highly derived post-embryonic development mode, it is difficult to incorporate these forms into the current model. However, looking at the cases where there is an embryonic nauplius (egg-nauplius) helps clarify the situation. As mentioned above, many crustaceans exhibit a slightly different mode of segmentation in the anterior few gnathal/trunk segments, suggesting that there is an anterior tagma that is distinct from the SAZ-driven sequentially segmenting posterior tagma. The evolution of head larvae involved an extreme heterochronic shift in the time of hatching relative to segment formation. The postponement of segmentation to the post-embryonic period obscures the different segmentation modes, and they may even be lost in some lineages. The view articulated by Fusco & Minelli [1] is that tagmata cannot be homologized across arthropod classes. I argue that if all PEF tagmata are derived from an ancestral embryonic tagma that was defined embryonically in a PEF, they should be seen as homologous. Similarly, all SAZ-derived tagmata are homologous (it is already generally accepted that the PGS are homologous across arthropods). However, although similar terms are used in different lineages (cephalothorax, trunk), there is no way to unambiguously homologize specific segments or structures within a given tagma across arthropod phylogeny. When comparing species with the same number of segments in a specific tagma, it may be possible to equate a segment in a given position with a segment in the same position in a different species, but this should be done with caution and with consideration of the evolutionary history of the species being compared. The prevailing paradigm is that Hox genes are the earliest determinants of segment identity in arthropods. Specific Hox genes confer tagma fate (e.g. Antennapedia is responsible for thoracic fate). Data on the development of numerous arthropods reviewed above indicate that the difference between the thorax and abdomen in insects or between the prosoma and opisthosoma in arachnids is determined very early in development, before the segments are visible morphologically, even before the segmentation cascade is completed, and indeed before Hox gene expression begins in the relevant regions. There is no doubt that Hox genes have a role in specific segment identity and this is supported by an enormous body of evidence, not only from Drosophila melanogaster, but from many other species [93]. Nonetheless, we must reconsider their role in determining higher level identity (i.e. the distinction between segments belonging to different tagmata), based on the observation that these differences stem from very early embryonic differences. I suggest a two-phase model for segment identity determination. The first phase defines tagma identity based on embryonic differences in the segmentation process of segments in the different tagmata. The genes responsible for these differences are currently unknown. The second phase defines the morphological differences between the segments and is responsible for the development of segment- and tagma-specific modifications. This phase is largely driven by Hox genes. The level of integration and mutual regulation and feedback between these two processes is likewise unknown and can form the basis for a fruitful research agenda. The evolution and development of tagmosis have been discussed intermittently in the arthropod literature for decades, but there has never been an attempt to offer a synthetic model for tagmosis. Most of the data presented in this paper have been known for many years. Crucial pieces of the puzzle were provided by the more recent study of segmentation in hemimetabolous insects within the context of tagma identity. I have attempted to provide a model of tagmosis that takes into account morphology, embryonic and post-embryonic segmentation, developmental dynamics, phylogeny and data from the fossil record. I have attempted to identify the core conserved elements of the developmental basis of tagmosis, while disregarding the many lineage-specific variations in tagmosis that have mostly led to confusion in the field. The synthetic model I present provides a relatively simple explanation for the observed patterns of extant and fossil arthropod body plans and also opens a slew of new questions that can—and should—be studied experimentally in a range of arthropod species. This paper is the outcome of several years of work on different modes of segmentation in my lab, and would not have been possible without the work of many students. I will not list them all here, but their work is cited throughout the paper. I am grateful to my long-time friend and collaborator Greg Edgecombe for discussions and comments on an earlier version of this paper. This work did not require ethical approval from a human subject or animal welfare committee. Supplementary material is available online [94]. I have not used AI-assisted technologies in creating this article. A.C.: conceptualization, funding acquisition, writing—original draft, writing—review and editing. I declare I have no competing interests. The work in my lab was funded by the Israel Science Foundation grants no. 570/21 and no. 120/16.

1. Fusco G, Minelli A. 2013. Arthropod segmentation and tagmosis. In Arthropod biology and evolution (eds Minelli A, Boxshall G, Fusco G), pp. 197–221. Berlin, Germany: Springer. (10.1007/978-3-642-36160-9_9) [DOI] [Google Scholar] 2. Dunlop JA, Lamsdell JC. 2017. Segmentation and tagmosis in Chelicerata. Arthropod Struct. Dev. 46, 395–418. (10.1016/j.asd.2016.05.002) [DOI] [PubMed] [Google Scholar] 3. Brenneis G, Bogomolova EV, Arango CP, Krapp F. 2017. From egg to ‘no-body’: an overview and revision of developmental pathways in the ancient arthropod lineage Pycnogonida. Front. Zool. 14, 6. (10.1186/s12983-017-0192-2) [DOI] [PMC free article] [PubMed] [Google Scholar] 4. Minelli A. 2011. The Myriapoda. In Treatise on zoology: anatomy, taxonomy, biology. Leiden, The Netherlands: Brill. [Google Scholar] 5. Schram FR, Koenemann S. 2022. Evolution and phylogeny of pancrustace - a story of scientific method. Oxford, UK: Oxford University Press. [Google Scholar] 6. Wolfe JM, Luque J, Bracken-Grissom HD. 2021. How to become a crab: phenotypic constraints on a recurring body plan. BioEssays 43, 00020. (10.1002/bies.202100020) [DOI] [PubMed] [Google Scholar] 7. Grimaldi D, Engel MS. 2005. Evolution of the insects. Cambridge, UK: Cambridge University Press. [Google Scholar] 8. Ortega-Hernández J. 2015. Lobopodians. Curr. Biol. 25, R873–R875. (10.1016/j.cub.2015.07.028) [DOI] [PubMed] [Google Scholar] 9. Ou Q, Shu D, Mayer G. 2012. Cambrian lobopodians and extant onychophorans provide new insights into early cephalization in Panarthropoda. Nat. Commun. 3, 1261. (10.1038/ncomms2272) [DOI] [PMC free article] [PubMed] [Google Scholar] 10. Park TYS, et al. 2018. Brain and eyes of Kerygmachela reveal protocerebral ancestry of the panarthropod head. Nat. Commun. 9, 1019. (10.1038/s41467-018-03464-w) [DOI] [PMC free article] [PubMed] [Google Scholar] 11. Cong P, Daley AC, Edgecombe GD, Hou X. 2017. The functional head of the Cambrian radiodontan (stem-group Euarthropoda) Amplectobelua symbrachiata. BMC Evol. Biol. 17, 208. (10.1186/s12862-017-1049-1) [DOI] [PMC free article] [PubMed] [Google Scholar] 12. Daley AC, Edgecombe GD. 2014. Morphology of Anomalocaris canadensis from the burgess shale. J. Paleontol. 88, 68–91. (10.1666/13-067) [DOI] [Google Scholar] 13. Potin GJM, Daley AC. 2023. The significance of Anomalocaris and other Radiodonta for understanding paleoecology and evolution during the cambrian explosion. Front. Earth Sci. 11, 1160285. (10.3389/feart.2023.1160285) [DOI] [Google Scholar] 14. Ortega-Hernández J. 2016. Making sense of ‘lower’ and ‘upper’ stem-group Euarthropoda, with comments on the strict use of the name Arthropoda von Siebold, 1848. Biol. Rev. 91, 255–273. (10.1111/brv.12168) [DOI] [PubMed] [Google Scholar] 15. O’Flynn RJ, Liu Y, Hou X, Mai H, Yu M, Zhuang S, Williams M, Guo J, Edgecombe GD. 2023. The early Cambrian Kylinxia zhangi and evolution of the arthropod head. Curr. Biol. 33, 4006–4013.(10.1016/j.cub.2023.08.022) [DOI] [PubMed] [Google Scholar] 16. Chen JY, Zhou GQ, Edgecombe GD, Ramsköld L. 1995. Head segmentation in early cambrian Fuxianhuia: implications for Arthropod evolution. Science 268, 1339–1343. (10.1126/science.268.5215.1339) [DOI] [PubMed] [Google Scholar] 17. Yang J, Ortega-Hernández J, Butterfield NJ, Zhang XG. 2013. Specialized appendages in fuxianhuiids and the head organization of early euarthropods. Nature 494, 468–471. (10.1038/nature11874) [DOI] [PubMed] [Google Scholar] 18. Aria C, Caron JB. 2015. Cephalic and limb anatomy of a new Isoxyid from the burgess shale and the role of ‘stem bivalved Arthropods’ in the disparity of the frontalmost appendage. PLoS One 10, e0124979. (10.1371/journal.pone.0124979) [DOI] [PMC free article] [PubMed] [Google Scholar] 19. Lamsdell JC, Stein M, Selden PA. 2013. Kodymirus and the case for convergence of raptorial appendages in Cambrian arthropods. Naturwissenschaften 100, 811–825. (10.1007/s00114-013-1081-y) [DOI] [PubMed] [Google Scholar] 20. Hughes NC. 2003. Trilobite body patterning and the evolution of arthropod tagmosis. BioEssays 25, 386–395. (10.1002/bies.10270) [DOI] [PubMed] [Google Scholar] 21. Hughes NC. 2003. Trilobite tagmosis and body patterning from morphological and developmental perspectives. Integr. Comp. Biol. 43, 185–206. (10.1093/icb/43.1.185) [DOI] [PubMed] [Google Scholar] 22. Hughes NC, Minelli A, Fusco G. 2006. The ontogeny of trilobite segmentation: a comparative approach. Paleobiology 32, 602–627. (10.1666/06017.1) [DOI] [Google Scholar] 23. Waloszek D, Maas A. 2005. The evolutionary history of crustacean segmentation: a fossil-based perspective. Evol. Dev. 7, 515–527. (10.1111/j.1525-142X.2005.05056.x) [DOI] [PubMed] [Google Scholar] 24. Izquierdo-López A, Caron JB. 2024. The Cambrian Odaraia alata and the colonization of nektonic suspension-feeding niches by early mandibulates. Proc. R. Soc. B 291, 20240622. (10.1098/rspb.2024.0622) [DOI] [PMC free article] [PubMed] [Google Scholar] 25. Briggs DEG, Parry LA. 2022. Putting heads together. Science 378, 831–832. (10.1126/science.add7372) [DOI] [PubMed] [Google Scholar] 26. Ortega-Hernández J, Janssen R, Budd GE. 2017. Origin and evolution of the panarthropod head: a palaeobiological and developmental perspective. Arthropod Struct. Dev. 46, 354–379. (10.1016/j.asd.2016.10.011) [DOI] [PubMed] [Google Scholar] 27. Lev O, Chipman AD. 2021. Development of the pre-gnathal segments in the milkweed bug Oncopeltus fasciatus suggests they are not serial homologs of trunk segments. Front. Cell Dev. Biol. 9, 695135. (10.3389/fcell.2021.695135) [DOI] [PMC free article] [PubMed] [Google Scholar] 28. Dearden PK, Akam M. 2001. Early embryo patterning in the grasshopper, Schistocerca gregaria: wingless, decapentaplegic and caudal expression. Development 128, 3435–3444. (10.1242/dev.128.18.3435) [DOI] [PubMed] [Google Scholar] 29. Choe CP, Miller SC, Brown SJ. 2006. A pair-rule gene circuit defines segments sequentially in the short-germ insect Tribolium castaneum. Proc. Natl Acad. Sci. USA 103, 6560–6564. (10.1073/pnas.0510440103) [DOI] [PMC free article] [PubMed] [Google Scholar] 30. Donoughe S, Extavour CG. 2016. Embryonic development of the cricket Gryllus bimaculatus. Dev. Biol. 411, 140–156. (10.1016/j.ydbio.2015.04.009) [DOI] [PubMed] [Google Scholar] 31. Bar-Lev Viterbo A, Wexler JR, Mayost Lev-Ari O, Chipman AD. 2024. Early embryonic development of the German cockroach Blattella germanica. bioRxiv (10.1101/2024.07.08.602440)) [DOI] [PMC free article] [PubMed] [Google Scholar] 32. Chipman AD, Arthur W, Akam M. 2004. Early development and segment formation in the centipede, Strigamia maritima (Geophilomorpha). Evol. Dev. 6, 78–89. (10.1111/j.1525-142x.2004.04016.x) [DOI] [PubMed] [Google Scholar] 33. Brena C, Akam M. 2012. The embryonic development of the centipede Strigamia maritima. Dev. Biol. 363, 290–307. (10.1016/j.ydbio.2011.11.006) [DOI] [PubMed] [Google Scholar] 34. Damen WGM, Weller M, Tautz D. 2000. Expression patterns of hairy, even-skipped, and runt in the spider Cupiennius salei imply that these genes were segmentation genes in a basal arthropod. Proc. Natl Acad. Sci. USA 97, 4515–4519. (10.1073/pnas.97.9.4515) [DOI] [PMC free article] [PubMed] [Google Scholar] 35. Stollewerk A, Schoppmeier M, Damen WGM. 2003. Involvement of notch and delta genes in spider segmentation. Nature 423, 863–865. (10.1038/nature01682) [DOI] [PubMed] [Google Scholar] 36. Damen WG, Janssen R, Prpic NM. 2005. Pair rule gene orthologs in spider segmentation. Evol. Dev 7, 618–628. (10.1111/j.1525-142X.2005.05065.x) [DOI] [PubMed] [Google Scholar] 37. Liu PZ, Kaufman TC. 2004. Krüppel is a gap gene in the intermediate germband insect Oncopeltus fasciatus and is required for development of both blastoderm and germband-derived segments. Development 131, 4567–4579. (10.1242/dev.01311) [DOI] [PubMed] [Google Scholar] 38. Ben-David J, Chipman AD. 2010. Mutual regulatory interactions of the trunk gap genes during blastoderm patterning in the hemipteran Oncopeltus fasciatus . Dev. Biol. 346, 140–149. (10.1016/j.ydbio.2010.07.010) [DOI] [PubMed] [Google Scholar] 39. Chipman AD. 2017. Oncopeltus fasciatus as an evo-devo research organism. Genesis 55, e23020. (10.1002/dvg.23020) [DOI] [PubMed] [Google Scholar] 40. Stahi R, Chipman AD. 2016. Blastoderm segmentation in Oncopeltus fasciatus and the evolution of insect segmentation mechanisms. Proc. R. Soc. B 283, 20161745. (10.1098/rspb.2016.1745) [DOI] [PMC free article] [PubMed] [Google Scholar] 41. Auman T, Chipman AD. 2018. Growth zone segmentation in the milkweed bug Oncopeltus fasciatus sheds light on the evolution of insect segmentation. BMC Evol. Biol 18, 178. (10.1101/327106) [DOI] [PMC free article] [PubMed] [Google Scholar] 42. Auman T, Vreede BMI, Weiss A, Hester SD, Williams TA, Nagy LM, Chipman AD. 2017. Dynamics of growth zone patterning in the milkweed bug Oncopeltus fasciatus. Development 144, 1896–1905. (10.1242/dev.142091) [DOI] [PMC free article] [PubMed] [Google Scholar] 43. Miyawaki K, Mito T, Sarashina I, Zhang HJ, Shinmyo Y, Ohuchi H, Noji S. 2004. Involvement of Wingless/Armadillo signaling in the posterior sequential segmentation in the cricket, Gryllus bimaculatus (Orthoptera), as revealed by RNAi analysis. Mech. Dev. 121, 119–130. (10.1016/j.mod.2004.01.002) [DOI] [PubMed] [Google Scholar] 44. Nakamoto A, Hester SD, Constantinou SJ, Blaine WG, Tewksbury AB, Matei MT, Nagy LM, Williams TA. 2015. Changing cell behaviours during beetle embryogenesis correlates with slowing of segmentation. Nat. Commun. 6, 6635. (10.1038/ncomms7635) [DOI] [PubMed] [Google Scholar] 45. Rosenberg MI, Brent AE, Payre F, Desplan C. 2014. Dual mode of embryonic development is highlighted by expression and function of Nasonia pair-rule genes. eLife 3, e01440. (10.7554/elife.01440) [DOI] [PMC free article] [PubMed] [Google Scholar] 46. Taylor SE, Dearden PK. 2022. The Nasonia pair-rule gene regulatory network retains its function over 300 million years of evolution. Development (Rome) 149, 199632. (10.1242/dev.199632) [DOI] [PMC free article] [PubMed] [Google Scholar] 47. Tautz D. 1988. Regulation of the Drosophila segmentation gene hunchback by two maternal morphogenetic centres. Nature 332, 281–284. (10.1038/332281a0) [DOI] [PubMed] [Google Scholar] 48. Jaeger J, Manu J. 2012. Drosophila blastoderm patterning. Curr. Opin. Genet. Dev. 22, 533–541. (10.1016/j.gde.2012.10.005) [DOI] [PubMed] [Google Scholar] 49. Chipman AD. 2020. The evolution of the gene regulatory networks patterning the Drosophila Blastoderm. Curr. Top. Dev. Biol. 139, 297–324. (10.1016/bs.ctdb.2020.02.004) [DOI] [PubMed] [Google Scholar] 50. Scholtz G. 2000. Evolution of the nauplius stage in Malacostracan crustaceans. J. Zool. Syst. Evol. Res 38, 175–187. (10.1046/j.1439-0469.2000.383151.x) [DOI] [Google Scholar] 51. Jirikowski G, Wolff C, Richter S. 2015. Evolution of eumalacostracan development—new insights into loss and reacquisition of larval stages revealed by heterochrony analysis. EvoDevo 6, 4. (10.1186/2041-9139-6-4) [DOI] [PMC free article] [PubMed] [Google Scholar] 52. Jirikowski GJ, Richter S, Wolff C. 2013. Myogenesis of Malacostraca—the ‘egg-nauplius’ concept revisited. Front. Zool. 10, 76. (10.1186/1742-9994-10-76) [DOI] [PMC free article] [PubMed] [Google Scholar] 53. Eriksson BJ, Ungerer P, Stollewerk A. 2013. The function of Notch signalling in segment formation in the crustacean Daphnia magna (Branchiopoda). Dev. Biol. 383, 321–330. (10.1016/j.ydbio.2013.09.021) [DOI] [PubMed] [Google Scholar] 54. Mittmann B, Ungerer P, Klann M, Stollewerk A, Wolff C. 2014. Development and staging of the water flea Daphnia magna (Straus, 1820; Cladocera, Daphniidae) based on morphological landmarks. EvoDevo 5, 12. (10.1186/2041-9139-5-12) [DOI] [PMC free article] [PubMed] [Google Scholar] 55. Dohle W, Scholtz G. 1988. Clonal analysis of the crustacean segment: the discordance between genealogical and segmental borders. Development 104, 147–160. (10.1242/dev.104.supplement.147)3253055 [DOI] [Google Scholar] 56. Scholtz G, Dohle W. 1996. Cell lineage and cell fate in crustacean embryos: a comparative approach. Int. J. Dev. Biol. 40, 211–220. [PubMed] [Google Scholar] 57. Wolff C. 2009. The embryonic development of the malacostracan crustacean Porcellio scaber (Isopoda, Oniscidea). Dev. Genes Evol. 219, 545–564. (10.1007/s00427-010-0316-6) [DOI] [PubMed] [Google Scholar] 58. Hejnol A, Scholtz G. 2004. Clonal analysis of Distal-less and engrailed expression patterns during early morphogenesis of uniramous and biramous crustacean limbs. Dev. Genes Evol. 214, 473–485. (10.1007/s00427-004-0424-2) [DOI] [PubMed] [Google Scholar] 59. Hejnol A, Schnabel R, Scholtz G. 2006. A 4D-microscopic analysis of the germ band in the isopod crustacean Porcellio scaber (Malacostraca, Peracarida)—developmental and phylogenetic implications. Dev. Genes Evol. 216, 755–767. (10.1007/s00427-006-0105-4) [DOI] [PubMed] [Google Scholar] 60. Vilpoux K, Sandeman R, Harzsch S. 2006. Early embryonic development of the central nervous system in the Australian crayfish and the Marbled crayfish (Marmorkrebs). Dev. Genes Evol. 216, 209–223. (10.1007/s00427-005-0055-2) [DOI] [PubMed] [Google Scholar] 61. Gerberding M, Browne WE, Patel NH. 2002. Cell lineage analysis of the amphipod crustacean Parhyale hawaiensis reveals an early restriction of cell fates. Development 129, 5789–5801. (10.1242/dev.00155) [DOI] [PubMed] [Google Scholar] 62. Browne WE, Price AL, Gerberding M, Patel NH. 2005. Stages of embryonic development in the amphipod crustacean,Parhyale hawaiensis. Genesis 42, 124–149. (10.1002/gene.20145) [DOI] [PubMed] [Google Scholar] 63. Kettle C, Arthur W. 2000. Latitudinal cline in segment number in an arthropod species, Strigamia maritima. Proc. R. Soc. B 267, 1393–1397. (10.1098/rspb.2000.1155) [DOI] [PMC free article] [PubMed] [Google Scholar] 64. Chipman AD, Arthur W, Akam M. 2004. A double segment periodicity underlies segment generation in centipede development. Curr. Biol. 14, 1250–1255. (10.1016/j.cub.2004.07.026) [DOI] [PubMed] [Google Scholar] 65. Brena C, Akam M. 2013. An analysis of segmentation dynamics throughout embryogenesis in the centipede Strigamia maritima. BMC Biol. 11, 112. (10.1186/1741-7007-11-112) [DOI] [PMC free article] [PubMed] [Google Scholar] 66. Janssen R, Prpic NM, Damen WGM. 2004. Gene expression suggests decoupled dorsal and ventral segmentation in the millipede Glomeris marginata (Myriapoda: Diplopoda). Dev. Biol. 268, 89–104. (10.1016/j.ydbio.2003.12.021) [DOI] [PubMed] [Google Scholar] 67. Damen WGM. 2002. Parasegmental organization of the spider embryo implies that the parasegment is an evolutionary conserved entity in arthropod embryogenesis. Development 129, 1239–1250. (10.1242/dev.129.5.1239) [DOI] [PubMed] [Google Scholar] 68. Akiyama-Oda Y, Oda H. 2006. Axis specification in the spider embryo: dpp is required for radial-to-axial symmetry transformation and sog for ventral patterning. Development 133, 2347–2357. (10.1242/dev.02400) [DOI] [PubMed] [Google Scholar] 69. Oda H, Nishimura O, Hirao Y, Tarui H, Agata K, Akiyama-Oda Y. 2007. Progressive activation of Delta-Notch signaling from around the blastopore is required to set up a functional caudal lobe in the spider Achaearanea tepidariorum. Development 134, 2195–2205. (10.1242/dev.004598) [DOI] [PubMed] [Google Scholar] 70. Gainett G, Sharma PP. 2020. Genomic resources and toolkits for developmental study of whip spiders (Amblypygi) provide insights into arachnid genome evolution and antenniform leg patterning. EvoDevo 11, 18. (10.1186/s13227-020-00163-w) [DOI] [PMC free article] [PubMed] [Google Scholar] 71. Gainett G, Crawford AR, Klementz BC, So C, Baker CM, Setton EVW, Sharma PP. 2022. Eggs to long-legs: embryonic staging of the harvestman Phalangium opilio (Opiliones), an emerging model arachnid. Front. Zool. 19, 11. (10.1186/s12983-022-00454-z) [DOI] [PMC free article] [PubMed] [Google Scholar] 72. Constantinou SJ, Duan N, Nagy LM, Chipman AD, Williams TA. 2020. Elongation during segmentation shows axial variability, low mitotic rates, and synchronized cell cycle domains in the crustacean, Thamnocephalus platyurus. EvoDevo 11, 1. (10.1186/s13227-020-0147-0) [DOI] [PMC free article] [PubMed] [Google Scholar] 73. Copf T, Rabet N, Celniker SE, Averof M. 2003. Posterior patterning genes and the identification of a unique body region in the brine shrimp Artemia franciscana. Development 130, 5915–5927. (10.1242/dev.00835) [DOI] [PubMed] [Google Scholar] 74. Copf T, Schröder R, Averof M. 2004. Ancestral role of caudal genes in axis elongation and segmentation. Proc. Natl Acad. Sci. USA 101, 17711–17715. (10.1073/pnas.0407327102) [DOI] [PMC free article] [PubMed] [Google Scholar] 75. Vilpoux K, Waloszek D. 2003. Larval development and morphogenesis of the sea spider Pycnogonum litorale (Ström, 1762) and the tagmosis of the body of Pantopoda. Arthropod Struct. Dev. 32, 349–383. (10.1016/j.asd.2003.09.004) [DOI] [PubMed] [Google Scholar] 76. Hou J, Hopkins MJ. 2024. New evidence for five cephalic appendages in trilobites and implications for segmentation of the trilobite head. Palaeontology 67, e12723. (10.1111/pala.12723) [DOI] [Google Scholar] 77. Walossek D, Müller KJ. 1998. Cambrian ‘Orsten’-type arthropods and the phylogeny of Crustacea. In Arthropod relationships (eds Fortey RA, Thomas RH), pp. 139–153. Dordrecht, The Netherlands: Springer. (10.1007/978-94-011-4904-4_12) [DOI] [Google Scholar] 78. Maas A, et al. 2006. The ‘Orsten’—more than a Cambrian Konservat-Lagerstätte yielding exceptional preservation. Palaeoworld 15, 266–282. (10.1016/j.palwor.2006.10.005) [DOI] [Google Scholar] 79. Moysiuk J, Caron JB. 2022. A three-eyed radiodont with fossilized neuroanatomy informs the origin of the arthropod head and segmentation. Curr. Biol. 32, 3302–3316.(10.1016/j.cub.2022.06.027) [DOI] [PubMed] [Google Scholar] 80. Moysiuk J, Caron JB. 2024. A quantitative assessment of ontogeny and molting in a Cambrian radiodont and the evolution of arthropod development. Paleobiology 50, 2023. (10.1017/pab.2023.18) [DOI] [Google Scholar] 81. Fu DJ, Zhang XL, Budd GE, Liu W, Pan XY. 2014. Ontogeny and dimorphism of Isoxys auritus (Arthropoda) from the early Cambrian Chengjiang biota, South China. Gondwana Res. 25, 975–982. (10.1016/j.gr.2013.06.007) [DOI] [Google Scholar] 82. Liu C, Fu D, Zhang X. 2022. Developmental dynamics is revealed in the early Cambrian arthropod Chuandianella ovata. iScience 25, 103591. (10.1016/j.isci.2021.103591) [DOI] [PMC free article] [PubMed] [Google Scholar] 83. Liu Y, Haug JT, Haug C, Briggs DEG, Hou X. 2014. A 520 million-year-old chelicerate larva. Nat. Commun. 5, 5440. (10.1038/ncomms5440) [DOI] [PubMed] [Google Scholar] 84. Liu Y, Melzer RR, Haug JT, Haug C, Briggs DEG, Hörnig MK, He YY, Hou XG. 2016. Three-dimensionally preserved minute larva of a great-appendage arthropod from the early Cambrian Chengjiang biota. Proc. Natl Acad. Sci. USA 113, 5542–5546. (10.1073/pnas.1522899113) [DOI] [PMC free article] [PubMed] [Google Scholar] 85. Fu D, Ortega-Hernández J, Daley AC, Zhang X, Shu D. 2018. Anamorphic development and extended parental care in a 520 million-year-old stem-group euarthropod from China. BMC Evol. Biol. 18, 147. (10.1186/s12862-018-1262-6) [DOI] [PMC free article] [PubMed] [Google Scholar] 86. Chipman AD. 2015. An embryological perspective on the early arthropod fossil record. BMC Evol. Biol. 15, 285. (10.1186/s12862-015-0566-z) [DOI] [PMC free article] [PubMed] [Google Scholar] 87. Wolfe JM. 2017. Metamorphosis is ancestral for crown euarthropods, and evolved in the Cambrian or earlier. Integr. Comp. Biol. 57, 499–509. (10.1093/icb/icx039) [DOI] [PubMed] [Google Scholar] 88. Davis GK, Patel NH. 2002. Short, long, and beyond: molecular and embryological approaches to insect segmentation. Annu. Rev. Entomol. 47, 669–699. (10.1146/annurev.ento.47.091201.145251) [DOI] [PubMed] [Google Scholar] 89. Sander K. 1976. Specification of the basic body pattern in insect embryogenesis. Adv. In Insect Phys 12, 125–238. (10.1016/S0065-2806(08)60255-6) [DOI] [Google Scholar] 90. Krause G. 1939. Die Eytypen der Insekten. Biol Zbl 59, 495–536. [Google Scholar] 91. Posnien N, Bucher G. 2010. Formation of the insect head involves lateral contribution of the intercalary segment, which depends on Tc-labial function. Dev. Biol. 338, 107–116. (10.1016/j.ydbio.2009.11.010) [DOI] [PubMed] [Google Scholar] 92. Scholtz G, Edgecombe GD. 2006. The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. Dev. Genes Evol. 216, 395–415. (10.1007/s00427-006-0085-4) [DOI] [PubMed] [Google Scholar] 93. Hughes CL, Kaufman TC. 2002. Hox genes and the evolution of the arthropod body plan. Evol. Dev. 4, 459–499. (10.1046/j.1525-142X.2002.02034.x) [DOI] [PubMed] [Google Scholar] 94. Chipman A. 2025. Supplementary material from: The development and evolution of arthropod tagmata. Figshare. (10.6084/m9.figshare.c.7750316) [DOI]

This section collects any data citations, data availability statements, or supplementary materials included in this article. Supplementary material is available online [94].