7-1-2021

Phylogeny and Evolutionary History of the Amniote Egg

J. M. Starck
Ludwig-Maximilians-Universität München

James R. Stewart
Ludwig-Maximilians-Universität München, stewarjr@etsu.edu

Daniel G. Blackburn
Trinity College Hartford

Citation Information

Phylogeny and Evolutionary History of the Amniote Egg

Copyright Statement

© 2021 The Authors.Journal of Morphologypublished by Wiley Periodicals LLC.

Creative Commons License

REVIEW

Phylogeny and evolutionary history of the amniote egg

J. Matthias Starck[1] | James R. Stewart[1,2] | Daniel G. Blackburn[3]

[1]Department of Biology, Ludwig-Maximilians-University Munich, Planegg-Martinsried, Germany

[2]Department of Biological Sciences, East Tennessee State University, Johnson City, Tennessee, USA

[3]Department of Biology, Trinity College, Hartford, Connecticut, USA

Correspondence
J. Matthias Starck, Department of Biology II, Ludwig-Maximilians-University Munich, Planegg-Martinsried, Germany.
Email: starck@lmu.de

Abstract

We review morphological features of the amniote egg and embryos in a comparative phylogenetic framework, including all major clades of extant vertebrates. We discuss 40 characters that are relevant for an analysis of the evolutionary history of the vertebrate egg. Special attention is given to the morphology of the cellular yolk sac, the eggshell, and extraembryonic membranes. Many features that are typically assigned to amniotes, such as a large yolk sac, delayed egg deposition, and terrestrial reproduction have evolved independently and convergently in numerous clades of vertebrates. We use phylogenetic character mapping and ancestral character state reconstruction as tools to recognize sequence, order, and patterns of morphological evolution and deduce a hypothesis of the evolutionary history of the amniote egg. Besides amnion and chorioallantois, amniotes ancestrally possess copulatory organs (secondarily reduced in most birds), internal fertilization, and delayed deposition of eggs that contain an embryo in the primitive streak or early somite stage. Except for the amnion, chorioallantois, and amniote type of eggshell, these features evolved convergently in almost all major clades of aquatic vertebrates possibly in response to selective factors such as egg predation, hostile environmental conditions for egg development, or to adjust hatching of young to favorable season. A functionally important feature of the amnion membrane is its myogenic contractility that moves the (early) embryo and prevents adhering of the growing embryo to extraembryonic materials. This function of the amnion membrane and the liquid-filled amnion cavity may have evolved under the requirements of delayed deposition of eggs that contain developing embryos. The chorioallantois is a temporary embryonic exchange organ that supports embryonic development. A possible evolutionary scenario is that the amniote egg presents an exaptation that paved the evolutionary pathway for reproduction on land. As shown by numerous examples from anamniotes, reproduction on land has occurred multiple times among vertebrates—the amniote egg presenting one "solution" that enabled the conquest of land for reproduction.

KEYWORDS
allantois, amnion, chorion, evolution, extraembryonic membranes, morphology, yolk sac

1 | INTRODUCTION

The structure of the egg and the extraembryonic membranes characterize the taxon Amniota. Amniota were recognized early (e.g., Haeckel, 1866; Gegenbaur, 1870; review of history in: Blackburn & Stewart, 2021), long before a strict phylogenetic toolkit (e.g., Hennig, 1966) was available. Today, the conjoint occurrence of amnion, chorion, allantois, and cellular yolk sac is considered a complex and highly integrated autapomorphic character (Ax, 2003; Mickoleit, 2004). Of course, the taxon Amniota is well corroborated by osteological (e.g., Gauthier et al., 1988) and molecular (e.g., Hasegawa, 2017) characters. The structure of the egg and the extraembryonic membranes of Amniota are often considered the key to their evolutionary success. Specifically, the conquest of terrestrial habitats for reproduction has been related to the occurrence of an amniotic egg (e.g., Romer, 1957; Carroll, 1970, 1991; Luckett, 1977; Packard & Seymour, 1997; but see discussion(s) in: Kohring, 1995; Laurin & Reisz, 1997; Wilkinson & Nussbaum, 1998; Laurin & Girondot, 1999; Laurin, 2005, 2010; Laurin et al., 2000; Skulan, 2000; Martin & Carter, 2013).

The avian egg stands almost paradigmatic as the standard example of an amniote egg. However, considerable morphological, physiological, and ecological diversity exists among amniote eggs (e.g., Packard and Packard (1980); Packard and Seymour (1997); Blackburn (1982, 1985, 2000, 2005); Deeming (2004); Blackburn and Flemming (2009), and Stewart (2013) for functional and physiological perspectives on the diversity of amniote eggs especially among squamates). Many features typically assigned to the amniote egg are in fact autapomorphic for modern birds (Neornithes), but do not characterize the amniote egg. Even a superficial overview of egg structures in other clades of (extant) sauropsids uncovers a considerable morphological diversity of eggshells, shell membranes, structure and composition of yolk and albumen, and the extraembryonic membranes. This morphological diversity of eggs accompanies a remarkable diversity of reproductive modes.

An increase in data related to egg structure and extraembryonic membranes of various groups of sauropsids in recent years (e.g., reviews in Blackburn, 2020; Stewart, 2020) coupled with continued exploration of phylogenetic relationships (see below) suggests that a summary of the current state of knowledge presented in a phylogenetic framework would be informative. Therefore, we analyze in detail the morphological diversity of amniote and vertebrate eggs, map the observed features on an existing phylogeny, reconstruct the ground pattern (= ancestral state reconstruction) of the eggs for the major clades of vertebrates, and trace the evolutionary history of the amniote egg.

The phylogenetic relationships among amniote taxa are currently controversial, with three major hypotheses; especially the position of Chelonia is uncertain (e.g., Hedges, 2012; Laurin & Reisz, 1997). Gauthier et al. (1988) considered turtles the sister taxon to a clade containing Lepidosauria and Archosauria. This topology has gained wide acceptance among morphologists and paleontologists (Laurin &

Reisz, 1995; Lee, 1997) and was relatively recently supported by developmental data (Werneburg & Sánchez-Villagra, 2009). An alternative hypothesis with turtles as diapsids and sister to lepidosaurs (Hill, 2005; Rieppel, 2000; Rieppel & DeBraga, 1996) has also gained wide acceptance. Recent molecular phylogenies support a phylogenetic position of turtles among diapsids and recognize lepidosaurs as a basal branch of sauropsids, while turtles are sister to archosaurs (Archelosauria; e.g., Zardoya & Meyer, 1998; Iwabe et al., 2005; Chiari et al., 2012; Field et al., 2014; Crawford et al., 2015).

The fact that the stem group of Tetrapoda branches into Amphibia and Amniota, and both groups differ substantially in egg morphology complicates ancestral state reconstruction for Amniota. Therefore, our comparison includes Dipnoi as the extant outgroup to Tetrapoda (Tetrapoda + Dipnoi = Choanata; Ax, 2003) to evaluate the ancestral character state in these basal branches. However, because characters such as megalecithal eggs, meroblastic cleavage, and a cellular yolk sac also occur in Myxinidae, Chondrichthyes, some Actinopterygii, and Coelacanthiformes (Latimeria) the ancestral character state reconstruction of these characters ultimately has to consider the phylogenetic root of vertebrates.

No doubt, as long as the phylogenetic relationships among Amniota (especially among Sauropsida) are not resolved, and as long as our knowledge of egg morphology and early development of some taxa remains incomplete, insights and explanations gained from this analysis remain temporary. However, by recognizing gaps in our knowledge, this review provides focus for future research.

A note on methods: this article reviews published data on reproductive morphology as completely as possible and maps the recognized characters on an existing phylogeny of the vertebrates. As is the nature of scientific data and inherent to a review of published material, information about species is scattered, heterogeneous in detail, and imbalanced on a taxonomic level, because original research was not based on a common theme and focus. Some major clades are represented only by few species and variation is often not grasped; small taxa might appear overrepresented because of their key-position in the current phylogenetic system. While this requires generalizations and represents a certain limitation for interpretations, it also highlights the need for more homogenous and complete data sampling.

The phylogram we use is derived from the morphological phylogenetic analysis by Ax (1984) and Mickoleit (2004) and is compatible with other recent (partial) phylogenies (e.g., Laurin & Reisz, 1997). The phylogenetic hypotheses presented by Ax (1984) and Mickoleit (2004) have the same topology of the cladogram (but differ slightly in the teminology). We deviate from those authors by considering cyclostomes (i.e., Myxinoidea, Petromyzonoidea) to be monophyletic (Kuraku et al., 1999; Kuratani & Ota, 2008a, 2008b). We use a conventional position of Chelonia as basal branch of Sauropsida (Gauthier et al., 1988; Laurin & Reisz, 1995; Lee, 1997; Werneburg & Sánchez-Villagra, 2009). Characters are discussed and morphologically validated (for possible convergence and parallel evolution) in the text;

they are summarized in Table 1 and, using parsimony principles, plotted on the phylogram. Of course, we are aware of conflicts and discussions that come with other hypotheses. However, since we had to decide for one phylogram as the basis for our review, we choose a conventional phylogeny. Results of our character mapping may differ when using another phylogenetic topology. This is an inherent problem when working with phylogenetic hypotheses. We make data, the phylogeny used, and the interpretations explicit, so that it may be adjusted to other phylogenetic hypotheses that might become available in future.

2 | LITERATURE REVIEW AND COMPARISONS

2.1 | Basal vertebrates

A large yolk, overgrown by a cellular yolk sac and meroblastic cleavage are often considered exclusive features of the amniote egg. However, a cellular yolk sac occurs in Cyclostomata, Chondrichthyes, numerous Actinopterygii, and a frog (*Eleuterodactylus coqui*; Elinson & Beckham, 2002). It is always associated with poly- or megalecithal eggs and, in clades that evolved (some form of) viviparity, may establish feto-maternal exchange structures. A correct ancestral character state reconstruction therefore has to consider those basal branches of the vertebrate phylogeny.

Cyclostomata: Cyclostomes is a monophyletic group that contains lampreys and hagfishes (e.g., Miyashita et al., 2019). Lampreys (Petromyzonoidea; Figure 1) have small, oligolecithal eggs, external fertilization, holoblastic cleavage, and incorporate yolk during blastula formation (*Lampetra fluviatilis*: plate 11 in Glaesner, 1910 [Figure 1]; *Lampetra* sp.: figures 65 and 69 in Pasteels, 1958; *Petromyzon planeri* (Figure 2): plate 28 in Kupffer, 1890 [Figures 1, 2]; *P. marinus*: Piavis, 1961, 1971; Richardson et al., 2010; Figure 4 in Richardson & Wright, 2003), such as basal Actinopterygii, Dipnoi and Amphibia. Species of Myxinoidea have megalecithal eggs (*Eptatretus stoutii* (Figure 3): Dean, 1898; *E. hexatrema*: Gilchrist, 1919; *Myxine* sp.: figures 22 and 23 in Walvig, 1963), with yolk being deposited in layers of yellow and white yolk (Riddle, 1911); meroblastic cleavage (Dean, 1899; Doflein, 1899; Gorbmann, 1997), and grow a cellular yolk sac (e.g., *E. stoutii*: plates 18 and 19 in Dean, 1899 [Figure 3]; *E. burgeri*: figure 11 in Ota & Kuratani, 2008). According to Miyashita and Coates (2015), the inner layer of the yolk sac is syncytial, and the outer layer carries large blood vessels. The topography of the blood vessels of the yolk sac, that is, two large anterior, one large posterior vitelline vessel and multiple, serial lateral blood vessels (cf. plates 18 and 19 in Dean, 1899; figure 11 in Ota & Kuratani, 2008 [Figure 3]) differs substantially from the topography of the yolk sac vessels described for any other vertebrate. Although the topography of the blood vessels has not been discussed in detail, its difference to the branching pattern of vitelline blood vessels found in other vertebrates is so striking that it might be considered evidence for an independent evolutionary origin of the cellular yolk sac and its vascularization in Myxinoidea. Despite megalecithal eggs and an amorphous ("horny") eggshell (with a micropyle; Walvig, 1963; Morisawa, 1999), hagfish eggs are most probably fertilized externally

(Gorbman, 1997; Miyashita & Coates, 2015; Powell et al., 2005). Because Petromyzonoidea and Myxinoidea differ in their egg morphology and cleavage pattern, a strict phylogenetic interpretation about the ancestral character state of Cyclostomata is possible only based on an outgroup comparison. Although it is beyond the scope of this review, a glimpse at eggs and early development of *Branchiostoma* (e.g., Freeman & Bracegirdle, 1982; *B. japonicum*: Hirakow & Kajita, 1990, 1991) or Tunicata (e.g., *Ascidiella aspersa*: Niermann-Kerkenberg & Hofmann, 1989; *Oikopleura dioica*: Stach et al., 2008; review in Stolfi & Brown, 2015) shows small eggs and holoblastic cleavage without formation of a yolk sac (= pattern observed in *Petromyzon*). This suggests external fertilization of small, oligolecithal eggs, with holoblastic cleavage and cellularization of the (few) yolk deposits as the ancestral character state for vertebrates (see also figure 1 in Elinson, 2009).

Chondrichthyes (Figure 4): All oviparous and many viviparous species of Chondrichthyes (Holocephali and Elasmobranchii) have large, hard-shelled eggs, where large yolk deposits provide nutrients for the developing embryo (reviews: Wourms, 1977; Carrier et al., 2004; Holocephali: review by Didier, 2004; *Hydrolagus colliei*: Dean, 1903, 1906 [plate 8 in Dean, 1906; Figure 4]; *Callorhinchus callorhynchus*: plate 12 in Schauinsland, 1903 [Figure 4]; *C. milii*: Didier et al., 1998). Egg cases are built by a regular three-dimensional network of collagen fibrils that is produced by the nidamental gland of the oviduct (Knupp et al., 1998; Luong et al., 1998). The egg case performs supportive, protective, and filtering functions for the embryo. Fertilization is internal with copulatory organs and cleavage patterns are meroblastic (*Dipturus batis* (Figure 5): see plates 14 and 15 in Balfour, 1876; *C. callorhynchus*: see plate XII, figures 89–97 in Schauinsland, 1903; *H. collie* see plates IV and V in Dean, 1906 [Figure 4]; *Squalus acanthias*: plate 1 in Scammon, 1911; *Scyliorhinus canicula*: Figures 2 and 3 in Ballard et al., 1993). Most probably, lecithotrophic oviparity is ancestral in Chondrichthyes, and various forms of viviparity including matrotrophic viviparity involving a yolk sac placenta evolved independently in several lines of Chondrichthyes (e.g., Lund, 1980; Hamlett et al., 2005; cf. Musick & Ellis, 2005). The histological organization of the lecithotrophic yolk sac has only rarely been described, but among those species that have been studied a high similarity has been reported (reviewed in Hamlett, 2005; four species of carcharhinid shark: Hamlett & Wourms, 1984; *Rhizoprionodon terraenovae*: Hamlett et al., 1987; *S. acanthias*: Jollie & Jollie, 1967; *Galeus melastomus*: Kondakova et al., 2016). A yolk syncytial layer borders internally the yolk sac endoderm. Immediately external to the endodermal epithelium occur granular cells that are either glandular, or hematopoietic in function, and relate directly to the vitelline blood vessels. The pattern of yolk sac blood vessels has not been studied but it differs substantially from that observed in Myxinoidea (compare Figures 3 and 5). The outer layers of the cellular yolk sac contain mesoderm derived smooth muscle cells, granular cells, and a fine layer of connective tissue. The yolk sac is externally (ectodermal) covered by a stratified epithelium (TeWinkel, 1943; figure 2 in Hamlett, 2005). Despite the scarce and scattered information, the histological organization of the yolk sac suggests an evolutionary origin in the stem group of Chondrichthyes independent from that of other vertebrates.
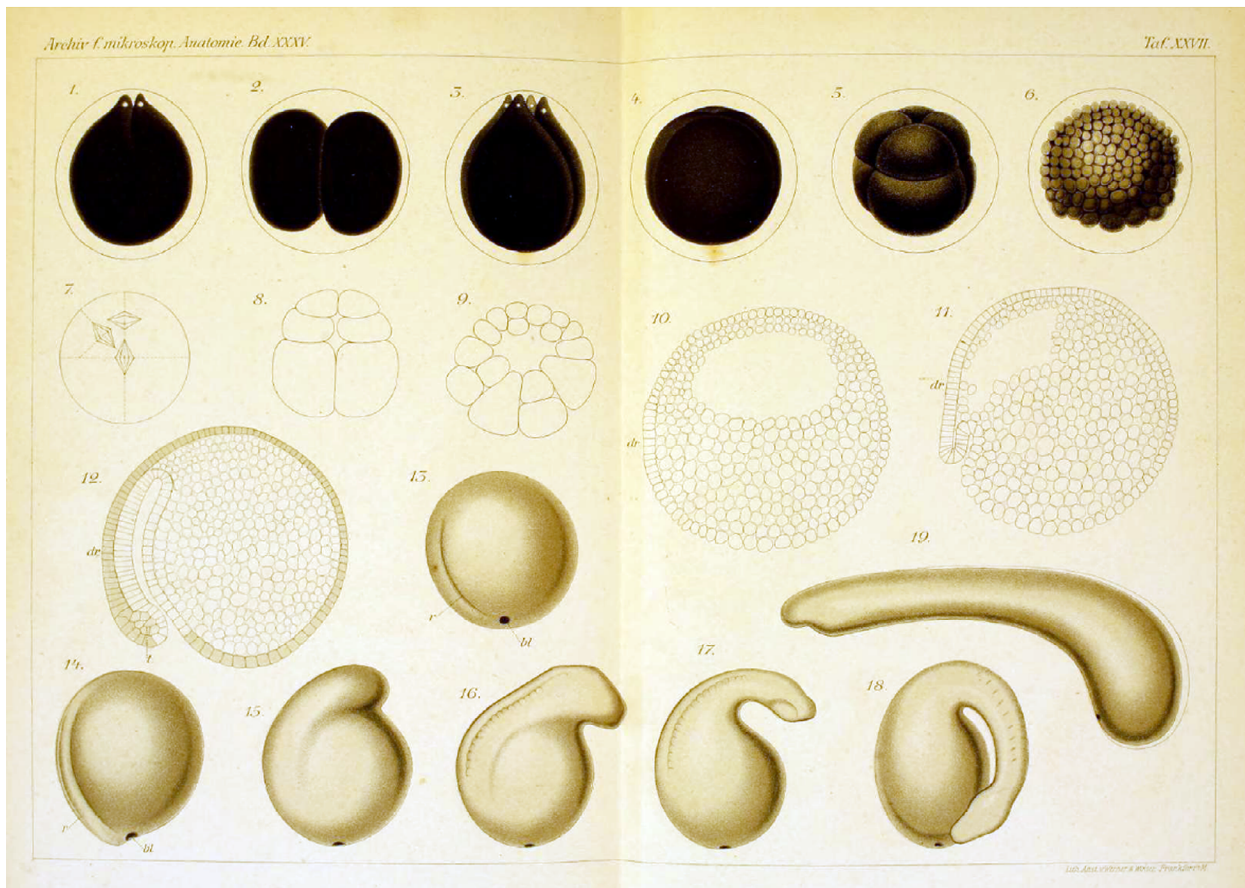
a
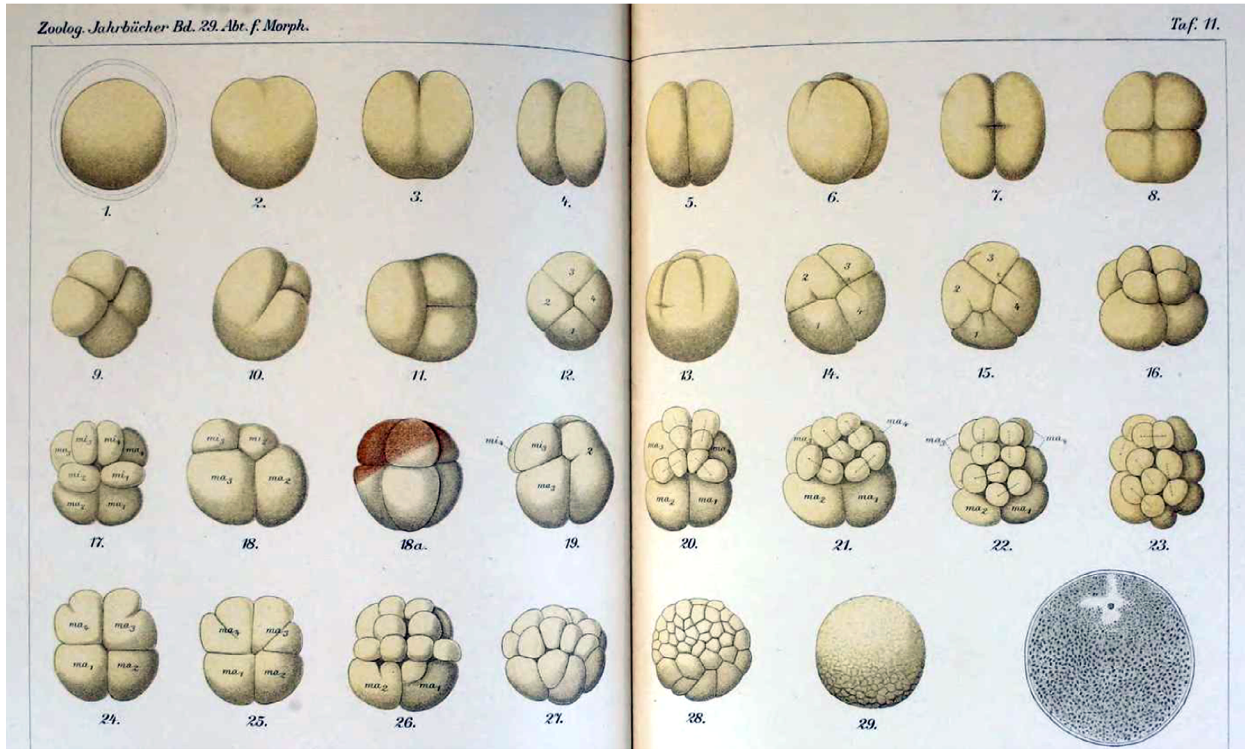
b

FIGURE 1 Legend on next page.

Actinopterygii: Egg morphology and early development in Actinopterygii (i.e., Cladistia, Chondrostei and Neopterygii [Lepisosteiformes, Amiiformes, Teleostei]) is important for a phylogenetic interpretation of egg morphology, cleavage pattern, and yolk sac structures in basal vertebrates. *Cladistia*: Bartsch et al. (1997) described the embryonic and larval development of *Polypterus senegalus*. Eggs are small and covered by an adhesive vitelline membrane (chorion of fish eggs). Fertilization is external. Cleavage is holoblastic and results in complete cellularization of yolk (similar to basal Amphibia; Kerr, 1907). *Chondrostei* also show holoblastic cleavage and patterns of gastrulation that resemble basal amphibian development (*Acipenser transmontanus*: Bolker, 1993a, 1993b; *A. baerii* (Figure 6): Park et al., 2013). Eggs are covered by a four-layered egg capsule, one layer being structurally identical to the jelly coat described for Amphibia (*A. transmontanus*; Cherr & Clark Jr., 1982).

Neopterygii (Figure 7): Lepisosteiformes: *Lepisosteus* sp. has relatively large eggs (~3 mm in *Lepisosteus osseus*; Long & Ballard, 2001) surrounded by a jelly coat are externally fertilized (Agassiz, 1879; Balfour & Parker, 1882). Long and Ballard (2001) reported that cleavage and incorporation of yolk during early development of *L. osseus* differ from that of other members of Neopterygii and Chondrostei. *Lepisosteus osseus* has relatively large eggs, with a well-defined egg membrane and jelly layer, incomplete (pseudo-meroblastic) cleavage (plate 21 in Balfour & Parker, 1882 [Figure 7]; figure 3A-D in Long & Ballard, 2001), and a well-defined yolk syncytial layer. *Lepisosteus osseus* embryos develop a vascularized yolk sac, but details of its histology and microscopic anatomy have not been documented. Egg morphology and early development are similar to those in teleosts (see also discussion in Elinson, 2009). *Amiiformes*: *Amia calva* (Figure 8) has relatively large (2.2 x 2.8 mm), oblong eggs covered by egg membranes as in *Lepisosteus* (Dean, 1896). Cleavage is unequal but holoblastic, and includes yolk into gigantic blastomeres (figures 13–19 and plate 19 in Whitman & Eycleshymer, 1897; Figure 8; Ballard, 1986). These yolky blastomeres are incorporated by epiboly. An overall similarity to amphibian development has been highlighted (Brachet, 1912 cit. in Ballard, 1986).

Teleostei: A vast diversity of developmental strategies and developmental modes characterizes teleost fishes. A phylogenetic analysis of reproductive morphology is not available but the features reported here characterize Teleostei as apomorphic features. By doing so, we do not try to fully characterize the teleost diversity in reproductive morphology. The relevant point here is that reproductive morphology of teleosts as a taxon is derived. Numerous teleost fishes have polylecithal eggs and develop an external cellular yolk sac. Teleost cleavage is meroblastic (review in Collazo et al., 1994; Desnitskiy, 2015). The yolk sac of teleost fishes is originally formed by the yolk syncytial layer, has no endodermal epithelium, and the yolk complex is not a component of the digestive system (e.g., Kondakova et al., 2017; Kondakova et al., 2019; Kondakova & Efremov, 2014). The yolk sac is later overgrown by epiboly from lateral folds of the early embryo (e.g., Carvalho & Heisenberg, 2010). The endodermal organizer, which is active during gastrulation, differs from that of the more basal Actinopterygii (Cooper & Virta, 2007). This, together with the divergent cytoarchitecture of the yolk sac of teleosts, suggests an independent evolutionary origin of meroblastic cleavage and the structure of the yolk sac in teleost fishes (Collazo et al., 1994; Desnitskiy, 2015, but see discussion in Elinson, 2009).

Coelacanthiformes: *Latimeria chalumnae* (Figure 9) has large eggs (8.5–9.0 cm diameter), cleavage is (not described) most certainly meroblastic, and it develops a cellular, vascularized yolk sac (Figure 9). The exterior surface of the yolk sac is lined by a single-layered, squamous epithelium that surrounds a bed of cortical sinuses. The inner surface is bounded by a layer of yolk-digesting cells. The interior surface of the sac is vascularized; no connection seems to exist between the interior of the yolk sac and the gut (Wourms et al., 1991). *Latimeria* is viviparous and embryos have been suggested to use both lecithotrophy and matrotrophy (Balon, 1991; Wourms et al., 1991). However, claims for matrotrophy have been rebutted by other researchers (Fricke & Frahm, 1992; Heemstra & Greenwood, 1992). Copulatory organs and even a cloaca are missing (Dingerkus et al., 1978). The derived features of the egg, the pattern of early

---

FIGURE 1 Petromyzonoidea, eggs and cleavage. (a) *Lampetra fluviatilis*, early development, holoblastic cleavage. Plate 11, figures 1–30 from Glaesner (1910). (1) fertilized egg with external protective layers. (2–5) consecutive images of formation during first cleavage; external layers not shown; (5) about 20 h post fertilization. (6) Beginning of second cleavage. (7) Same egg from top view. (8) slightly advanced stage of second cleavage. (9) Same egg from top view. (10, 11) Incomplete stage of second cleavage; 22–23 h post fertilization. (12) 4 cell stage, 24 h post fertilization. (13) Beginning of third, equatorial cleavage; 25 h post fertilization. (14, 15) two successive stages during 3rd cleavage. (16) 8-cell stage with unusual radial arrangement of the micromeres. (17–19) More frequently encountered arrangement of the 8-cell stage; 27–30 h post fertilization. (20) 12-cell stage; 31 h post fertilization. (21–23) Displacement of micromeres, in 22, 23 macromeres already in division; 32 h post fertilization. (24) Figure 22 from vegetal pole. (25) Somewhat later. (26) Division of macromeres *ma1* and *ma2*, *ma1* being somewhat advanced. (27–29) Three stages of blastula from lateral view. (30) Vertical section through an egg just before first cleavage. Caption translated from original (shortened and edited) [chiefly #1 above] by JMS. Glaesner, L. (1910). Studien zur Entwicklungsgeschichte von *Petromyzon fluviatilis*. *Zool. Jahrb. (Anat.)* 29, 139–190. Downloaded 25.08.2020 from biodiversity heritage library: https://www.biodiversitylibrary.org/page/11609919 (copyright in public domain). (b) *Petromyzon planeri*, early cleavage stages, gastrulation and early embryogenesis. Plate 27 from Kupffer (1890). (1–6) Cleavage stages of *P. planeri* drawn in translucent light; mag. 35:1. (7) Schematic drawing of the orientation of cleavages. (8) Cross-section through an egg at 12 h post fertilization. (9) Cross-section through an egg at 24 h post fertilization; mag. 35:1. (10) Beginning formation of the blastoderm on the dorsal side; mag. 60:1. (11, 12) Gastrulation; mag. 60:1. (13) Dorsal furrow (r), does not extend to the blastopore (bl); mag. 35:1. (14) Dorsal furrow on the bulging rudiment of the embryo. (15) Shape of the egg on the 4th day (Neapel); mag. 35:1. (16) Shape of egg and embryo at beginning of the sixth day (Neapel); mag. 35:1. (17) Embryo from the second half of the sixth day; mag. 35:1. (18) Embryo from the second half of the seventh day. Caption translated from original by JMS. Kupffer, C. (1890). Entwicklung von *Petromyzon planeri*. *Arch. Mik. Anat* 35, 469–558. Downloaded 12.2.2021 from biodiversity heritage library: https://www.biodiversitylibrary.org/page/14005544 (copyright in public domain)
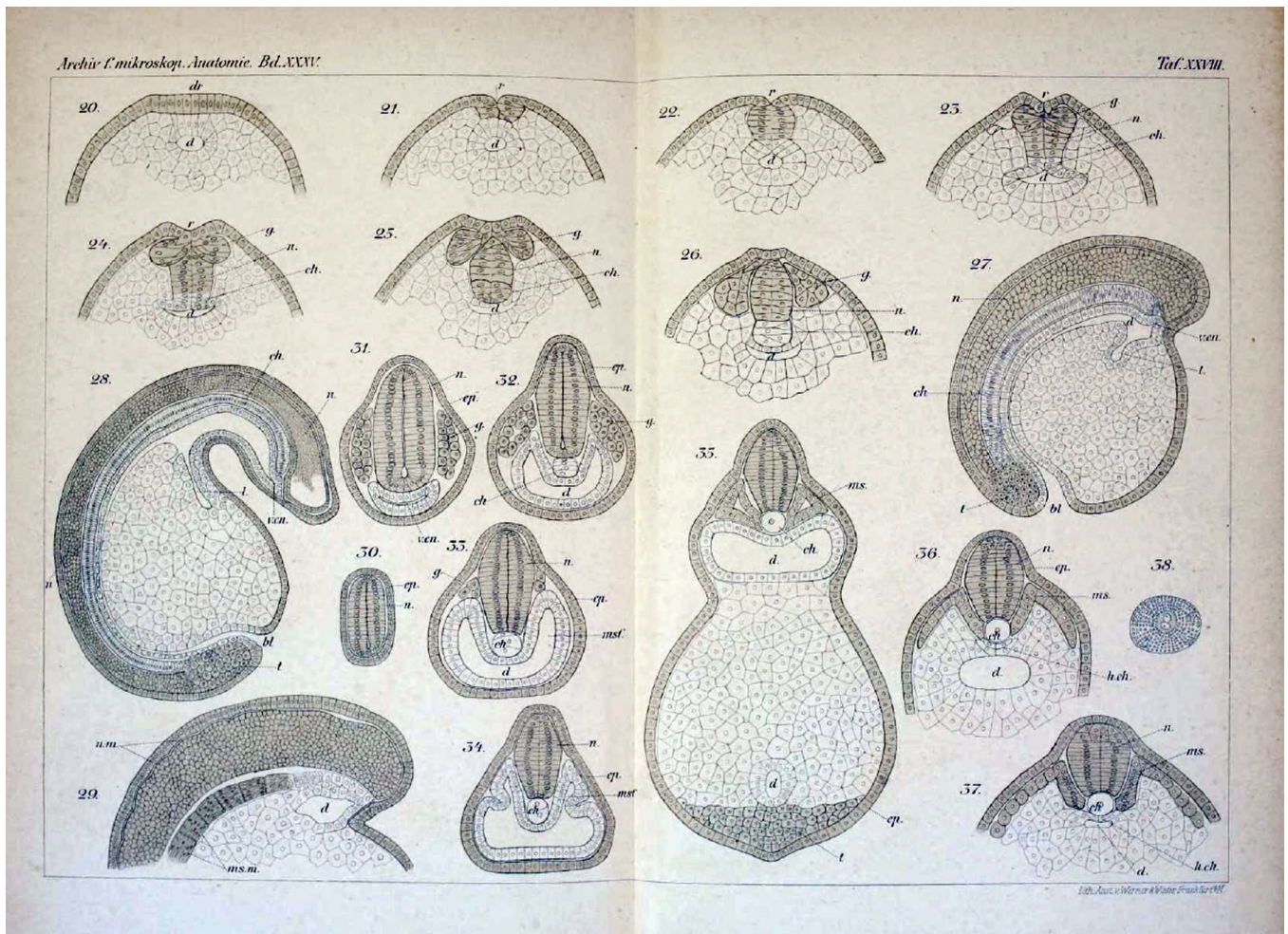
FIGURE 2 *Petromyzon planeri,* early development, holoblastic cleavage and yolk endoderm (Plate 28, from Kupffer, 1890). (20) Cross-section through the dorsal region of a gastrula. (21) Cross-section through the dorsal region at beginning upfolding of ectoderm. (22) Cross-section through the dorsal region of an egg during advanced formation of the primitive streak. (23, 24) Consecutive stage during formation of the primitive streak in the anterior region of the embryo. (25, 26) Cross-section through the anterior region of the embryo after differentiation into neural chord with paired ganglia and notochord. (27) Median sagittal section through an embryo at the end of fourth day. (28) Median sagittal section through an embryo at between 5th and 6th day. (29) Median sagittal section through an embryo at beginning of the third period (6th day). (30, 31, 32, 33, 34) Consecutive cross-sections through the head of an embryo in the 2nd period; 5th day. (35) Cross-section through the head and tail of an embryo in the 2nd period; 5th day. (36, 37) Cross-sections through the transition between head to trunk. Cells in the dorsal region of the neural chord are irregular. (38) A single cell of the notochord. the cytoplasm containing yolk cytoplasm is external, the yolk free cytoplasm with two nuclei is central. Abbreviations: bl, blastopore; ch, notochord; d, embryonic gut; dr, dorsal side; ep, epidermis; g, ganglion; hch, hypochord; ms, mesoderm; msf, mesoderm folds; msm, mesomeres; n, neural chord; nm, r, primitive groove; t, teloblast; ven, anterior endoderm pocket. Caption translated from original by JMS. Kupffer, C. (1890). Entwicklung von *Petromyzon planeri*. Arch. Mik. Anat 35, 469–558. . Downloaded 12.2.2021 from biodiversity heritage library: https://www.biodiversitylibrary.org/page/14005544 (copyright in public domain)

development of *Latimeria,* and the unknown features of the many extinct basal sarcopterygian taxa, make ancestral character reconstruction for Sarcopterygii a difficult task.

Dipnoi (Figure 10): Eggs of Dipnoi have been described as "heavily yolked, hemispherical in shape, and enclosed in a single vitelline and triple jelly envelope. The egg itself is about 3 mm across, with the jelly, 1 cm across" (*Neoceratodus forsteri*: Kemp, 1982, 1987, 1997, 2011). *Protopterus dolloi* also has a thick jelly coat, while the jelly coat in *Lepidosiren paradoxa* is reduced or vestigial (Kerr, 1900). The jelly coat is secreted by the oviduct and functions as a protective layer; there is no collagenous eggshell membrane. Fertilization is external. Cleavage

of the egg is holoblastic in all species (e.g., *N. forsteri*: figure 1 in Kemp, 1982; Figure 10; *L. paradoxa*: plate 8 and 9 in Kerr, 1900; Figure 10) but is irregular in *N. forsteri* (figures 1–3 in Kemp, 1982).

2.2 | Amphibia

In extant amphibians, the yolk is surrounded by a vitelline membrane and externally covered by a jelly coat (= egg capsule). Egg size (diameter) averages at ~2.5 mm (Desnitskiy, 2014), with a range between 0.5 and 10 mm (*Gastrotheca ceratophrys*; *G. weinlandii*; *Hemiphractus*

FIGURE 3 *Eptatretus stoutii*, early development and yolk sac development (plates XVIII and XIX from Dean, 1899 [figure and caption reprinted from Ota & Kuratani, 2008]). The figures in Plate XVIII are from preserved specimens, with the exception of those of the last two eggs. Figures 34 and 35 are drawn from the same embryo. Figures 48, 49, and 50 are from the same embryo. All the embryos in Plate XIX were drawn from live specimens. Figures 52, 53, and 54 are derived from the same embryo. The embryo in figure 70 is a late embryo, corresponding to that shown in Plate XIX, figure 66, drawn after this embryo was fixed. The head and tail of this embryo are shown lifted from the yolk sac. The late embryos in figures 61 and 65 correspond to the embryos in figures 126 and 127, respectively. The young specimen in figure 128 corresponds to that in figure 72. The late embryo (larva) at about the time of hatching was also drawn in figure 72, and this embryo corresponds to figure 128, Plate XXV. Dean, B. (1899). On the embryology of *Bdellostoma stouti*. A general account of myxinoid development from the egg and segmentation to hatching. In "Festschrift zum 70ten Geburtstag Carl von Kupffer" Gustav Fischer Verlag, Jena, pp 220–276. (copyright in public domain)

scutatus; del Pino & Escobar, 1981). The cleavage is holoblastic and unequal, resulting in yolk-rich vegetal cells. The yolk is completely cellularized during cleavage, and incorporated into the endoderm during gastrulation. No cellular yolk sac is formed. It is generally accepted that these features represent the group pattern of Amphibia (e.g., Duellman & Trueb, 1986) though each group contains species that deviate from this pattern. The structure of the amphibian egg and the early embryological development have been described for numerous species (e.g., *Lissotriton vulgaris* (Figure 11), Glaesner, 1925; *Andrias japonicas* (Figure 12), Kudo, 1938; *Ambystoma mexicanum*: Bordzilovskaya et al., 1989; *Rana pipiens*: Rugh, 1951; *Microhyla ornata*: Shimizu & Ota, 2003; *Microhyla fissipes*: Wang et al., 2017; generalized staging tables in Gosner, 1960; review in Desnitskiy, 2014; Desnitskiy & Litvinchuk, 2015). However, variation of egg size, cleavage pattern (Desnitskiy, 2014; Desnitskiy & Litvinchuk, 2015), and

morphology of the jelly coat in Anura and Caudata (Altig & McDiarmid, 2007; Salthe, 1963) suggest multiple independent evolutionary lines of diversification within these taxa. An enormous diversity of reproductive modes evolved in amphibian clades, including multiple evolutionary origins of internal fertilization (Sever et al., 2003), post-fertilization egg retention, direct development, origins of viviparity (e.g., Gower et al., 2008; Kupfer et al., 2016; Wake, 1972, 1977a, 1977b, 1992, 1986, 2015; Wilkinson & Nussbaum, 1998) and fully terrestrial reproduction (Goin & Goin, 1962; Wake, 1978). The cleavage pattern of species with comparatively large eggs (e.g., *Ensantina eschscholtzii*: egg diameter 6.1 mm; Collazo & Keller, 2010) is meroblastic until approximately the 16-cell stage. Eggs of *Gastrotheca rhiobambae* are 2.1–3.6 mm in diameter. First cleavage is total but later cleavages become irregular resulting in an embryonic disk (del Pino & Elinson, 1983; del Pino & Escobar, 1981, Elinson & del Pino, 1985).
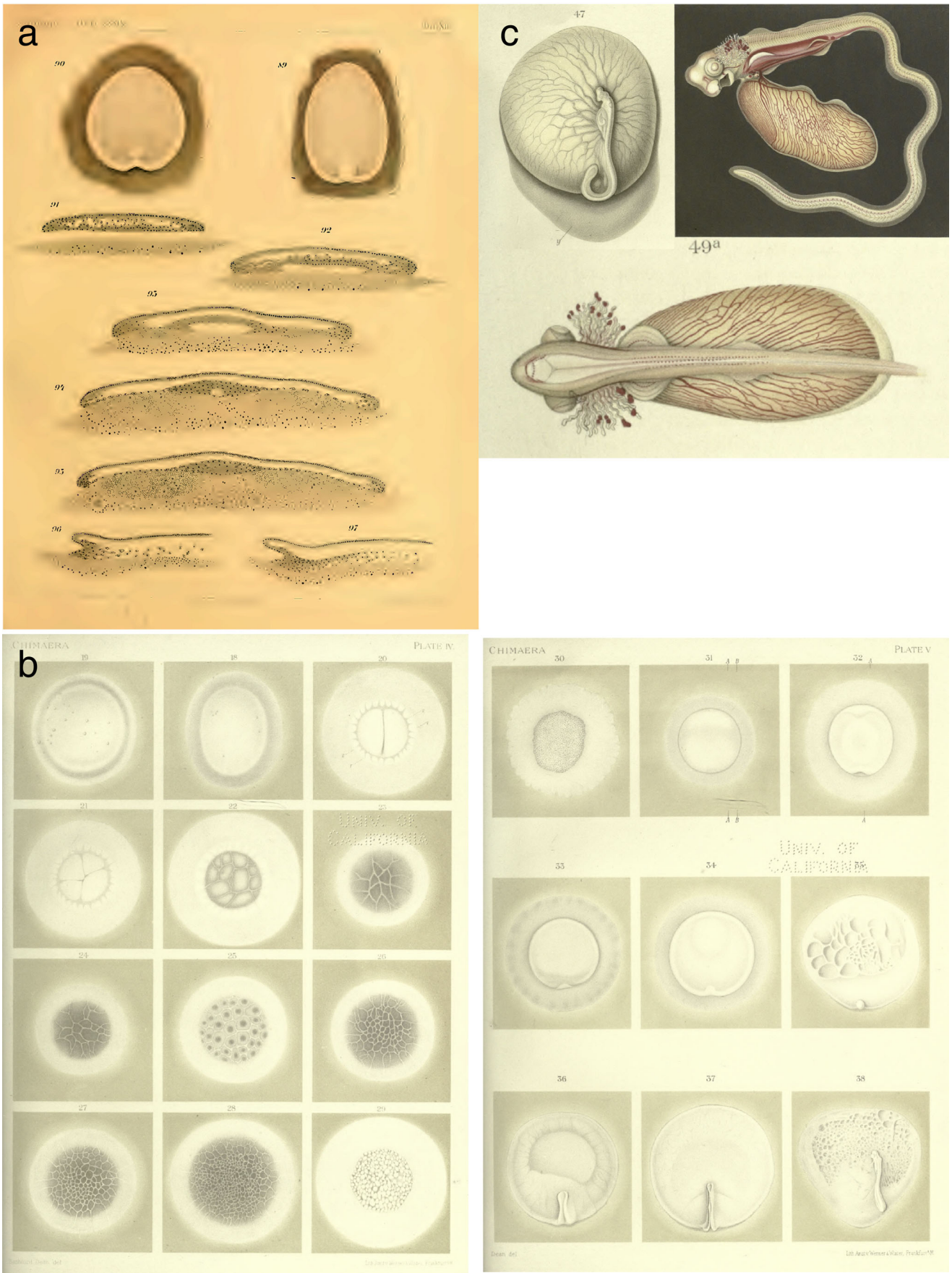
FIGURE 4   Legend on next page.

Eggs of *Eleutherodactylus coqui* have a diameter of ∼3.5 mm and meroblastic cleavage resulting in the formation of an embryonic disk, and the origin of a nutritional endoderm, that is, a tissue that provides nutrition, but does not differentiate into digestive tract tissue. This is a remarkable, independent origin of a "yolk sac-analogue" in amphibians (e.g., Buchholz et al., 2007; Elinson, 2009; Elinson & Beckham, 2002; Elinson & del Pino, 2012).

Caecilians show a considerable diversity of their reproductive strategies ranging from oviparity, through egg retention, direct development and viviparity including altricial and precocial young (Dünker et al., 2000; Kupfer et al., 2006; Kupfer et al., 2016). Internal fertilization has been reported for many species and is presumed for all species (e.g., Goin & Goin, 1962; Wake, 1977a, 1993, 2015) and even pseudo-meroblastic cleavage has been reported (*Ichthyophis glutinosus* (Figure 13): Sarasin & Sarasin, 1887; Svensson, 1938; *Hypogeophis rostratus*: Brauer, 1897; Dünker et al., 2000). Riddle (1911) reports that the polylecital eggs of *Ichtyophis* are structured into layer(s) of yellow and white yolk and have a central latebra. However, according to Kupfer et al. (2016) oviparity, holoblastic cleavage of yolk rich eggs, and lecithotrophic development of the embryo resulting in aquatic larvae, represent the developmental ground pattern of caecilians. Thus, it is highly probable that this also represents not only the ancestral character state of Amphibia, but, considering outgroup Dipnoi, also Tetrapoda. One may add that internal fertilization by means of intromittent organs (modifications of the male cloacal and body wall musculature; Wake, 1977b) are an autapomorphic feature of caecilians.

2.3 | Amniota

2.3.1 | Mammalia

The basal branch of Mammalia is Monotremata (Figure 14), the only group of mammals that lays eggs. The ovulated eggs of *Ornithorhynchus* are about 3.5–4 mm in diameter, are rich in yolk, and undergo meroblastic cleavage. Caldwell (1887) described the incomplete meroblastic cleavage, a feature found only in Monotremata among mammals, but

FIGURE 4 Chondrichthyes, Holocephali, drawings of cleavage and early developmental stages. (a) *Callorhinchus callorhynchus* (plate 12 from Schauinsland, 1903). (89, 90) Blastoderm (different proportions length/width are probably caused by dissection). (91–95) cross-sections through the posterior part of embryo shown in figure 90. Figure 91 is through the most posterior part of the embryo which is already elevated above the yolk. (96, 97) longitudinal sections through an embryo, which was considerably younger than the embryo shown in figure 89. Only the posterior part of the sections is drawn. Caption translated from original (shortened and edited) by JMS. Schauinsland, H. (1903). Beiträge zur Entwicklungsgeschichte und Anatomie der Wirbeltiere I. Sphenodon, Callorhynchus, Chamaeleo. *Zoologica* 39, 1–98. (Verlag Erwin Nägele, Stuttgart). Downloaded 20.10.2020 from Biodiversity Heritage Library https://doi.org/10.5962/bhl.title.11952 (copyright in public domain). (b) *Hydrolagus collie* (plates 4 and 5 from Dean, 1906). Plate 4: Stages of fertilization, segmentation and blastula (18) (preparations magnified about 15 diameters. All drawings from fresh material. Figures 22 to 28 from camera drawings of embryos which had been removed from the egg and viewed as transparent objects.) Figure 18. Late stage of fertilization. The oblong shape of the germinal area is due to artifact. The preparation illustrates the number and size of the entrance pits of spermatozoa and the extent of the marginal groove. Figure 19. Later stage of fertilization. This indicates the extent of the marginal groove and the difference in size of the entrance pits of the spermatozoa. Figure 20. Stage showing in surface view a single furrow. As already noted, however, this stage is not one of first segmentation, since it contains several segmentation nuclei. Surrounding the germinal area is a narrow groove margined outwardly by eminences containing sperm nuclei. Figure 21. Stage similar to foregoing, but showing at the surface four blastomeres. Figure 22. Stage of early segmentation. Here the marginal areas containing sperm nuclei are far less conspicuous. Figure 23. Stage similar to the preceding. Figure 24. Stage of segmentation. Figure 25. Stage of late segmentation. Blastomeres in resting stage. Figure 26. Stage of late segmentation. Figure 27. Stage of late segmentation. The darker color of the central blastomeres indicates a greater depth in this region of the germ. Figure 28. Blastula. In this stage inter-blastomeral lines were traced over the light-colored circumgerminal ring. Figure 29. Blastula. Viewed as an opaque object, and showing a sharply marked boundary between the blastoderm and the circumgerminal ring. Plate 5: Blastula, gastrula and early embryos. (preparations magnified about 15 diameters. In figures 30–34 the circumgerminal zone has been inaccurately lithographed; it should appear less conspicuous, its outer margin merging insensibly into the surrounding yolk.) figure 30. Late blastula, showing especially the extent of the circumgerminal ring and its irregular margin. Figure 31. Early gastrula. The transverse shadow at the lower end of the germinal area represents the beginnings of the archenteric cavity. Figure 32. Early gastrula, showing the extent of the archenteric space. Figure 33. Gastrula, showing the appearance of the head region of the embryo. In this preparation merocytes could be distinguished in the outer part of the circumgerminal ring. Figure 34. Gastrula, showing the early embryo and the extent of the segmentation cavity. Figure 35. Gastrula, slightly older, showing the early vascularization of the blastoderm. figure 36. Gastrula, showing early embryo at a stage corresponding with Balfour's stage C in the shark. Figure 37. Blastoderm, showing embryo at a stage corresponding with Balfour's stage F in the shark. Figure 38. Blastoderm and embryo at a stage corresponding with Balfour's stage G in the shark. Original caption from: Dean, B. (1906). *Chimaeroid fishes and their development* (no. 32). Carnegie Institution of Washington. pp. 1–194. Downloaded 20.10.2020 from Biodiversity Heritage Library https://doi.org/10.5962/bhl.title.29471 (copyright in public domain). (c) *Hydrolagus collie* (plate 8 from Dean, 1906). Figure 47. Embryo and blastoderm shown attached to irregular mass of yolk. The embryo is of the stage shown in plate vn, figure 44. It will be seen that a deep crease marks the line of separation of blastoderm and yolk, y. figure 49. Late embryo. Age unknown (probably five or 6 months), corresponding approximately to Balfour's stage N in shark. Although this specimen was examined living, and was apparently uninjured, its body cavity was filled with blood cells. Observe also the enlarged blood-knots in the external gills and the position of the spiracle denoted in this figure by the small red spot immediately above the rim of the upper jaw. (Embryo's length 35 mm.). Figure 49 a. dorsal aspect of preceding specimen. This pictures more clearly the blood-knots of the external gills. Original caption from: Dean, B. (1906). *Chimaeroid fishes and their development* (no. 32). Carnegie Institution of Washington. Pp. 1–194. Downloaded 20.10.2020 from biodiversity heritage library https://doi.org/10.5962/bhl.title.29471 (copyright in public domain)
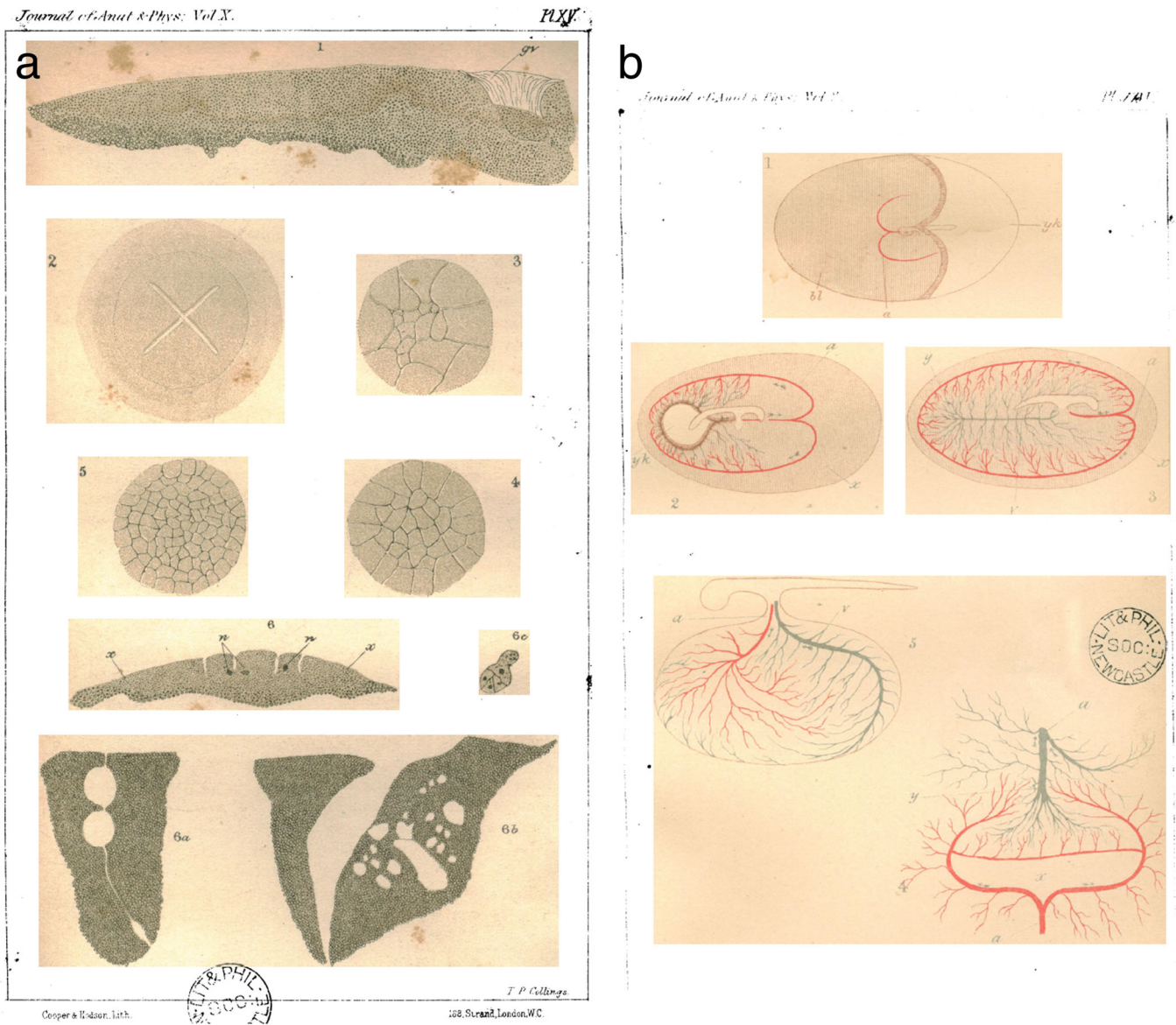
FIGURE 5 *Dipturus batis*, cleavage and early embryogenesis (plates 15 and 26 from Balfour, 1876). (a) (1) section through the germinal disc of a ripe ovarian ovum of the skate. (2) surface-view of a germinal disc with two furrows. (3, 4, 5) surface-views of three germinal discs in different stages of segmentation. (6) section through the germinal disc represented in (3). The engraver has in this figure not accurately copied my original drawings in respect to the structure of the segmentation-furrows. x. Edge of germinal disc. (6 a, b) two furrows of the same germinal disc more highly magnified. (6c) a nucleus from the same germinal disc highly magnified. (b) Plate 26, (1) yolk of a *Pristiurus* egg with blastoderm and embryo. About two-thirds of the yolk has been enveloped by the blastoderm. the embryo is still situated at the edge of the blastoderm, but at the end of a bay in the outline of this. The thickened edge of the blastoderm is indicated by a darker shading. Two arteries have appeared. (b) yolk of an older *Pristiurus* egg. The yolk has become all but enveloped by the blastoderm, and the embryo ceases to lie at the edge of the blastoderm, owing to the coalescence of the two sides of the bay which existed in the earlier stage. The circulation is now largely developed. it consists of an external arterial ring, and an internal venous ring, the latter having been developed in the thickened edge of the blastoderm. outside the arterial ring no vessels are developed. (c) the yolk has now become completely enveloped by the blastoderm. The arterial ring has increased in size. The venous ring has vanished, owing to the complete enclosure of the yolk by the blastoderm. the point where it existed is still indicated (y) by the brush-like termination of the main venous trunk in a number of small branches. (d) Diagrammatic projection of the vascular system of the yolk sac of a somewhat older embryo. The arterial ring has grown much larger and the portion of the yolk where no vessels exist is very small (x). The brush-like termination of the venous trunk is still to be noticed. the two main trunks (arterial and venous) in reality are in close contact as in Figure 5, and enter the somatic stalk close together. The letter *a* which points to the venous (blue) trunk should be v and not a. (e) circulation of the yolk sac of a still older embryo, in which the arterial circle has ceased to exist, owing to the space outside it having become smaller and smaller and finally vanished. Abbreviations: a, arteries of yolk sac (red); bi, blastoderm; gv, germinal vesicle; n; nucleus; v, veins of yolk sac (blue); x, portion of blastoderm outside the arterial circle in which no blood vessels are present; yk, yolk. Original, reformatted caption from Balfour, F. M. (1876). On the development of elasmobranch fishes: The general features of the elasmobranch embryo at successive stages. J. Anat. Physiol. 10:2–411. Downloaded 12.02.2021 from journal of anatomy, https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1319107/pdf/janatphys00196-0163.pdf and https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1319085/pdf/janatphys00197-0060.pdf (copyright in public domain)
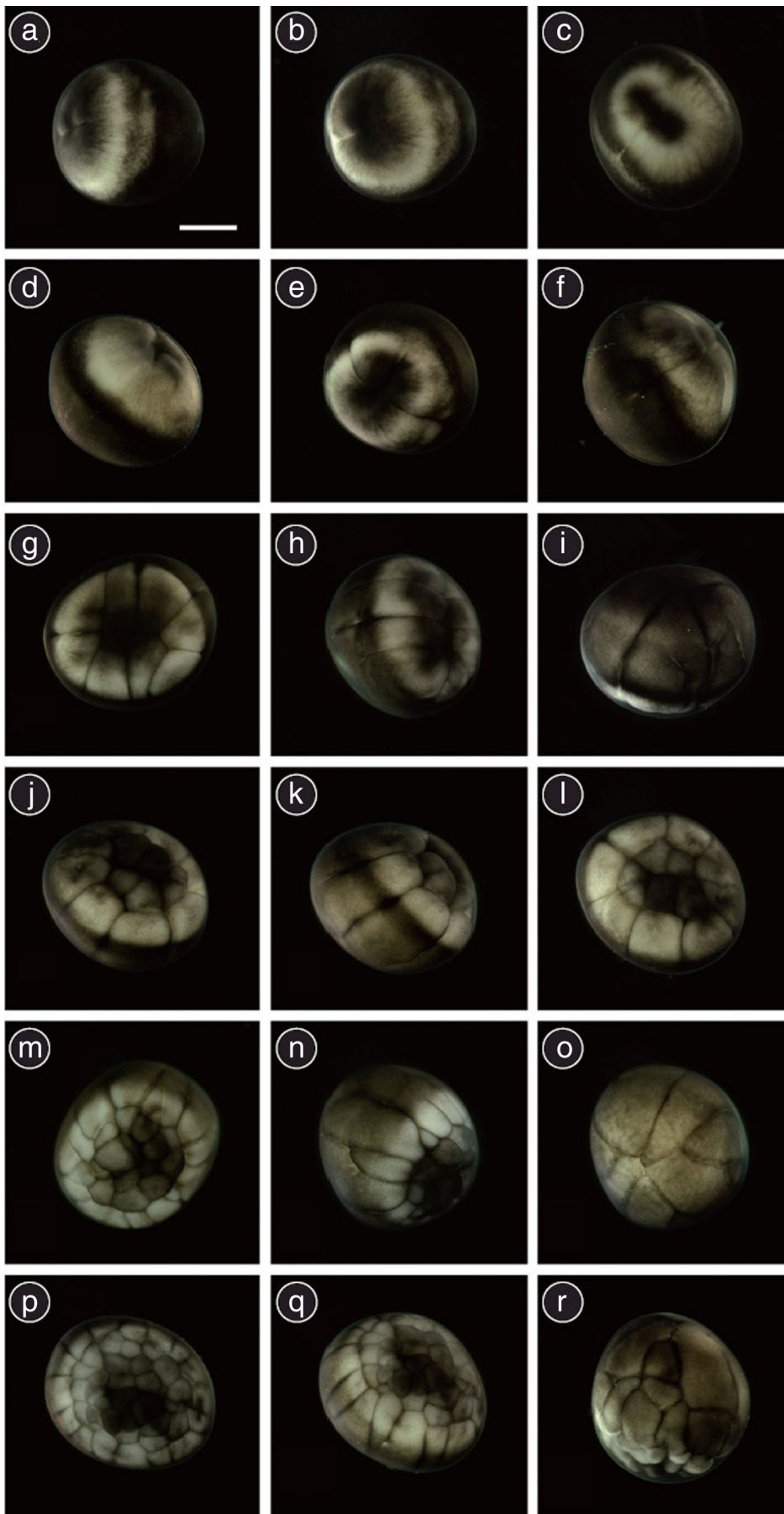
FIGURE 6 *Acipenser baerii*, early cleavages; figure 1 from Park et al. (2013). (a–c) First cleavage to form two cells. (d, e) Second cleavage in animal hemisphere (four cells). (f) Lateral view of four-celled embryo showing the partial infiltration of cleavage furrow into the vegetal hemisphere. (g, h) Eight cells in animal hemisphere. (i) Vegetal view of the embryos showing eight cells in the animal hemisphere. (j–l) embryos showing 16 cells in animal hemisphere. (m–o) irregular blastomeres formed after fifth cleavage in the animal hemisphere (animal view, lateral view and vegetal view, respectively). (p–r) continued cleavages in animal (p, q) and vegetal (r) hemispheres. Developmental time for each stage can be referred to table 1. Scale bar: A = 1 mm (a–r). Park, C., Lee, S. Y., Kim, D. S., & Nam, Y. K. (2013). Embryonic development of Siberian sturgeon *Acipenser baerii* under hatchery conditions: An image guide with embryological descriptions. *Fisheries and Aquatic Sciences*, 16(1), 15–23 (copy right: CC-BC, NC 3.0)
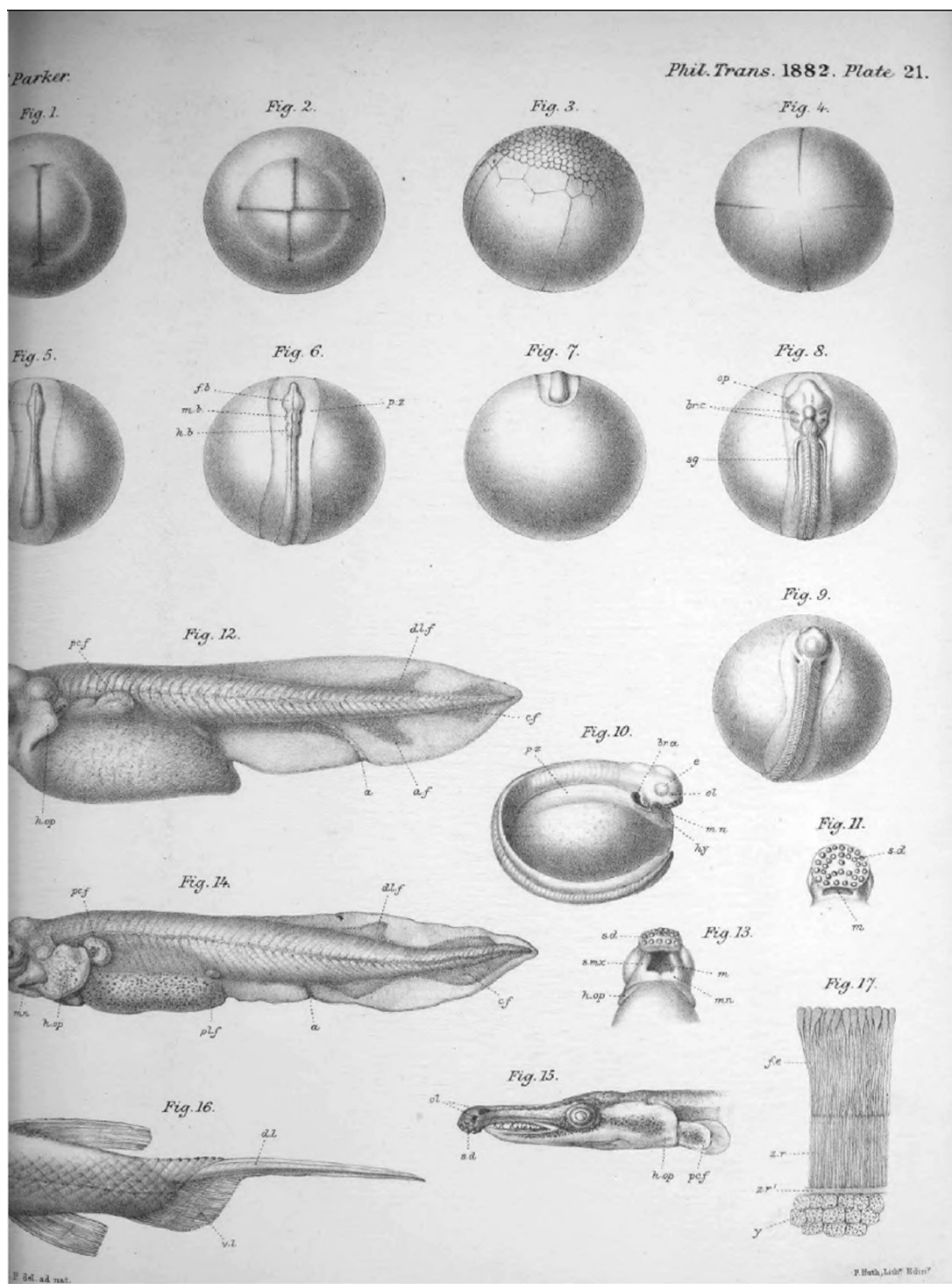
FIGURE 7 *Lepisosteus osseus*, cleavage and early embryogenesis. (1–4) Different stages in the segmentation of the ovum. (1) Ovum with a single vertical furrow, from above. (2) Ovum with two vertical furrows, from above. (3) Side view of an ovum with a completely formed blastodermic disc. (4) The same ovum as Figure 3, from below, showing four vertical furrows nearly meeting at the vegetative pole. (5–10) external views of embryos up to -time of hatching. Figure 5. Embryo, 3*5 mm long, third day after impregnation. (6) Embryo on the fifth day after impregnation. (7) Posterior part of same embryo as Figure 6, showing tail swelling. (8) Embryo on the sixth day after impregnation. (9) Embryo on the seventh day after impregnation. (10) Embryo on the eleventh day after impregnation (shortly before hatching). (11) Head of embryo about the same age as Figure 10, ventral aspect. (12) Side view of a larva about 11 mm in length, shortly after hatching. (13) Head of a larva about the same age as Figure 12, ventral aspect. (14) Side view of a larva about 15 mm long, 5 days after hatching. (15) Head of a larva 23 mm in length. (16) Tail of a larva 11 cm in length. (17) Transverse section through the egg-membranes of a just-laid ovum. (we are indebted to professor W. K. Parker for Figures 12, 14, and 15). Original, reformatted caption from Balfour, F. M. & Parker W. N. (1882). VII. On the structure and development of *Lepisosteus. Philos. Trans. Roy. Soc. 173, 359–442.* Downloaded 17.02.2021 from philosophical transactions of the Royal Society https://royalsocietypublishing.org/doi/pdf/10.1098/rstl.1882.0008 (copyright in public domain)

FIGURE 8 *Amia calva*, cleavage and early embryogenesis. (a) Figures 13–19 from Whitman and Eycleshymer (1897). (13) Oblique section of an egg in the stage of the fourth cleavage, just before the fifth cleavage. The plane of the section is represented by the dotted line 13–13 in (7). The se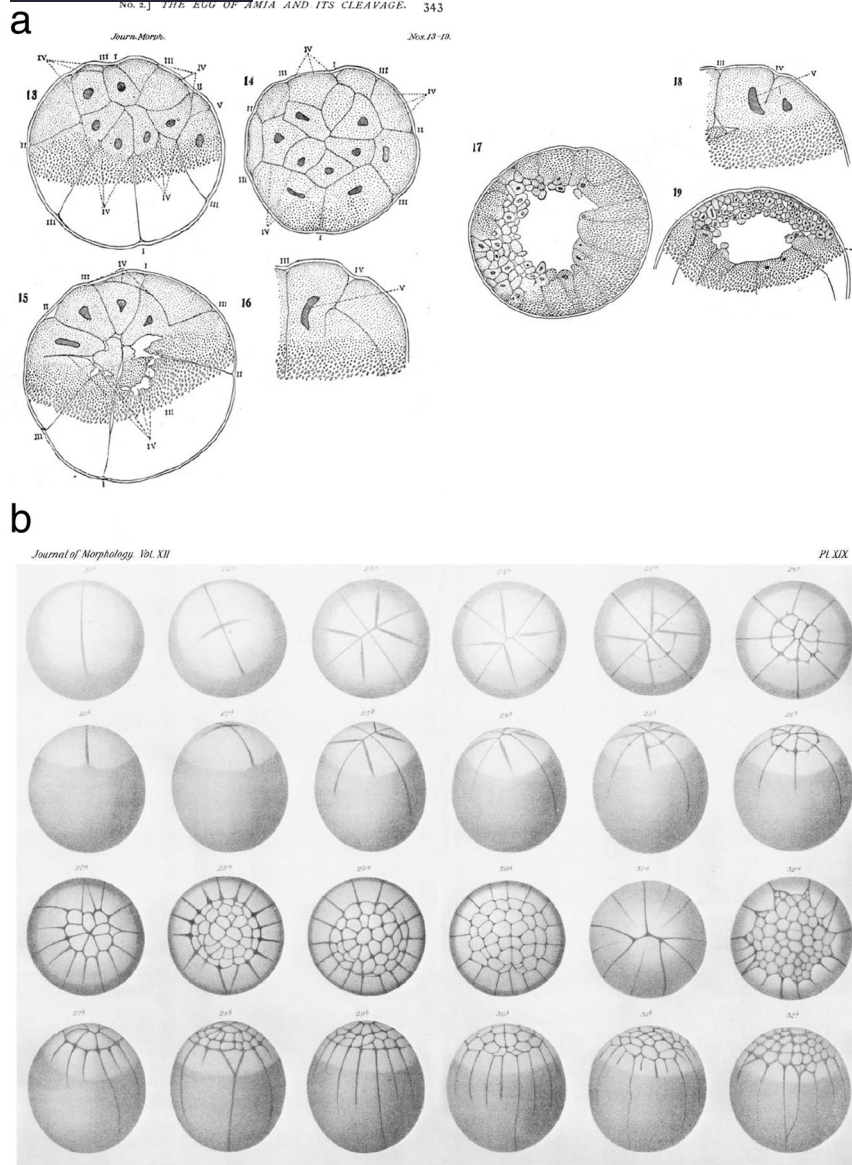ction shows on one side that the fourth cleavage has not yet cut off the central cells. (14) Oblique section of the same stage, passing along the line 14–14 of (6). The section shows the plane of elongation of the nuclei in the marginal segments, which are soon to be divided by a set of verticals, forming a part of the fifth cleavage. (15) Oblique section along the line 15-15- in (7). The section shows that the circular groove (IV) becomes continuous below with the vacuolar spaces. (16 and 18). Vertical sections of the calotte from different eggs in the stage of fourth cleavage. The sections show the vertical elongation of the nuclei of the central cells preparatory to the horizontal cleavage which is to divide them. (17) Oblique section of an egg in a stage a little earlier than that shown in (19). The section passes in the plane indicated by the line 17–17 in (15). The section shows an exceptionally large cleavage cavity. It also shows numerous yolk nuclei lying at the inner ends of the large yolk segments. (19) Vertical section of a typical blastula. The cleavage cavity in this egg is also exceptionally large. Some of the large yolk segments may be seen, dividing at their inner ends, the cells thus derived being continually added to the calotte. (b) Plate 19 from Whitman and Eycleshymer (1897)). All the figures were drawn from material fixed in chrom-osmic and preserved in 80% alcohol. (21a). View of the upper pole of the egg, showing the position of the first groove and micropylar orifice. (21b). Profile view of the same egg. (22a) View of the upper pole of the egg at the beginning of the second. (22b) Profile view of the same. (23a) View of the upper pole, showing symmetrical third verticals. (23b) Profile view of the same. (24a) View of the upper pole in same stage as (23), showing an asymmetrical position of one of the third verticals. (24b) Profile view of the same egg. (25a) The formation of the first set of circular grooves. (25b) Profile view of the same. (26a) The first set of circular grooves completed, and the fourth set of (26b) Profile view of the same. (27a) Fourth set of verticals well advanced. (27b) Profile view of the same. (28a) shows the addition of two new sets of circular grooves, one within, the other without, the first circular groove. (28b) Profile view of the same. (29a) A little later stage, showing another set of circular grooves outside of those seen in (28). (29b) Profile view of the same. (30a) About the same stage. (30b) Profile view of the same. (31a) The lower pole at about the same stage as figures 29 and 30. (31b) Profile view of the same. (32a) A later stage. (32b) Profile view of the same. Original, reformatted caption from Whitman, C. O., & Eycleshymer, A. C. (1897). The egg of *Amia* and its cleavage. Journal of Morphology, 12, 309–354. (reprinted under license number 5012441183133; 19.2.2021)
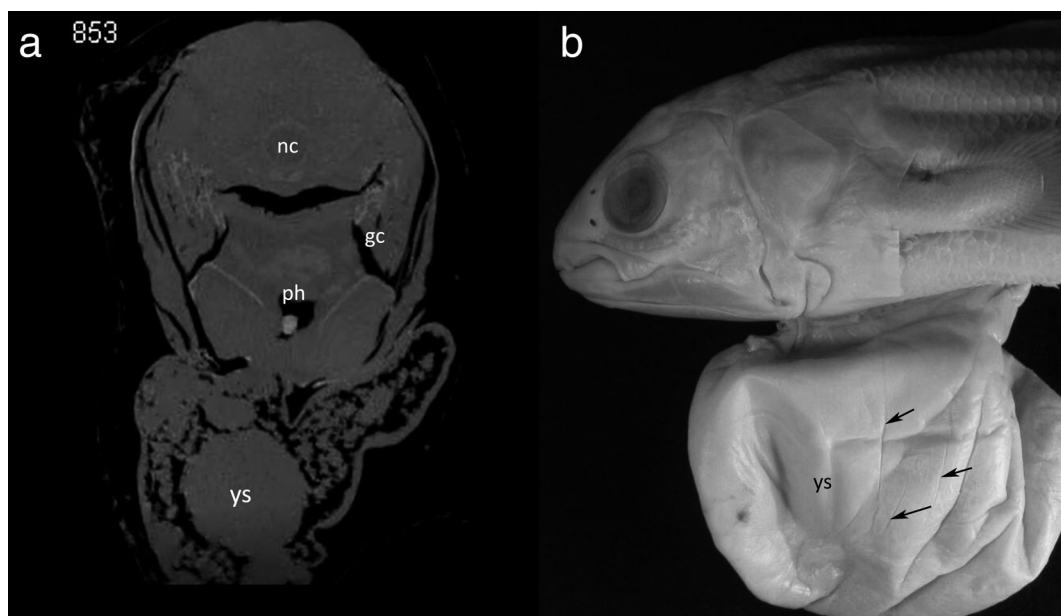
FIGURE 9 *Latimeria chalumnae*, late embryo. (a) CT-image, coronal slice (#853 of a complete series of 3649 images) throughthe yolk sac region. This specimen, a preserved embryo (AMNH 32949), is 308 mm long. It was found off Mutsamudu in Mozambique Channel (county-Anjouan Island; drainage-western central Indian coast; collected by native fisherman/G. Garrouste; field number Anthony-62-#26, 7/1/1962). (b) Photograph of the same individual showing the anterior part of the body and the yolk sac attached. Larger superficial blood vessels can be recognized macroscopically. Abbreviations: gc, gill chamber; nt, notochord; ph, pharyngeal region; ys, yolk sac. Arrows in (b) indicate major yolk sac blood vessels. Reference: Dr. Julian Humphries, 2002, "*Latimeria chalumnae*" (on-line), digital morphology. Accessed 12.2.2021 at http://digimorph.org/specimens/Latimeria_chalumnae/whole/. Reprinted with permission (19.03.2021 granted by J. Maisano)

shared with sauropsids. Gatenby (1922) reported details about the ripe egg of *Ornithorhynchus paradoxus*, including a description of the structuring of the yolk in an inner and an outer zone, and a latebra with a central core, a neck and enlarged upper area under the germinal disc (*O. paradoxus*: plate 12, figures 1, 3 in Gatenby, 1922; *Echidna aculeata*: plate 1, figures 1–9 in Semon, 1894; Figure 14). These observations have been confirmed (e.g., Gatenby & Hill, 1924; Flynn & Hill, 1939; Hughes, 1993; Menkhorst et al., 2009; Carter, 2021 in this issue of the Journal of Morphology) and compared with the occurrence of a latebra in the yolk in sauropsids (Caldwell, 1887) and presence of white yolk and a latebra in *Echidna* (Semon, 1894). The distinction between white and yellow yolk goes back to Schwann (1847). Both types of yolk primarily differ in the size of the yolk gobules and their subdroplets (small in white yolk, large in yellow yolk; Riddle, 1911; Bellairs, 1961; Chang et al., 1977; Perry & Gilbert, 1985). White yolk is found in the latebra, a thin superficial layer around the yolk ball, and in species with megalecital eggs is deposited in thin layers of yellow and white yolk. Layering follows a circadian pattern of yolk formation with the white yolk being deposited at night and yellow yolk during daytime (Bellairs, 1961, Conrad & Warren, 1939, Riddle, 1911, Romanoff & Romanoff, 1949). The occurrence of different layers of yolk is probably related to the size of the yolk ball and the duration of yolk deposition, it always occurs with megalecital eggs (Myxinoidea, Chondrichthyes, some Amphibia, Amniota).

A considerable part of the embryonic development is intrauterine, and egg laying is delayed (egg retention). During the extended uterine passage of the monotreme egg, a partially vascularized, cellular yolk sac grows over the yolk ball (e.g., figure 61 in Semon, 1894). The yolk is enclosed by a cellular yolk sac that grows primarily as a bilaminar omphalopleure, but subsequently becomes trilaminar by immigration of extraembryonic mesoderm. The nonvascularized area of the cellular yolk sac absorbs maternal secretions (Hughes, 1993; Hughes et al., 1977; Hughes & Hall, 1998) resulting in continued growth of the egg by absorption of uterine secretions. Upon laying, the egg has about 16–18 mm diameter. A thin three-layered eggshell is deposited around the egg toward the end of the uterine period (Hill, 1933; Hughes, 1984). When the egg is laid, it contains a ~19 somite embryo. Cells of the extraembryonic endoderm phagocytose yolk spheres, blood vessels form in the extraembryonic mesoderm, and the extraembryonic ectoderm remains flattened to cuboidal cells. The yolk sac is not only the site of nutrient uptake of yolk, but also the site of primary erythropoiesis. After egg laying, the extraembryonic ectoderm of the yolk sac supposedly becomes functional for gas exchange.

We do not discuss specific adaptations of the therian eggs because egg retention, intrauterine development, and the evolution of feto-maternal exchange organs in Metatheria and Eutheria resulted in modified morphologies of the egg as well as the extraembryonic membranes, that is, amnion, serosa, allantois, and cellular yolk sac. Despite their fascinating evolution and morphological diversity, feto-maternal exchange organs among metatherian and eutherian mammals are clearly clade specific apomorphic features and contribute little to the
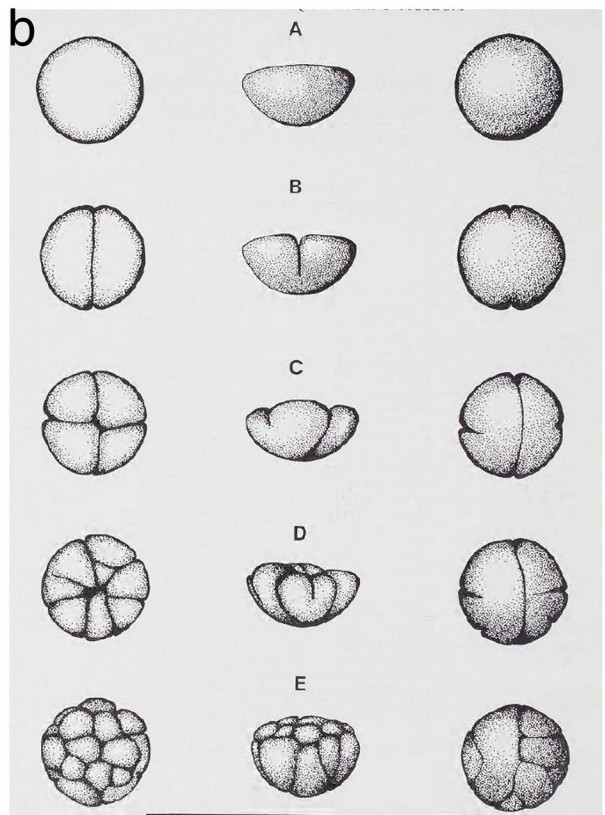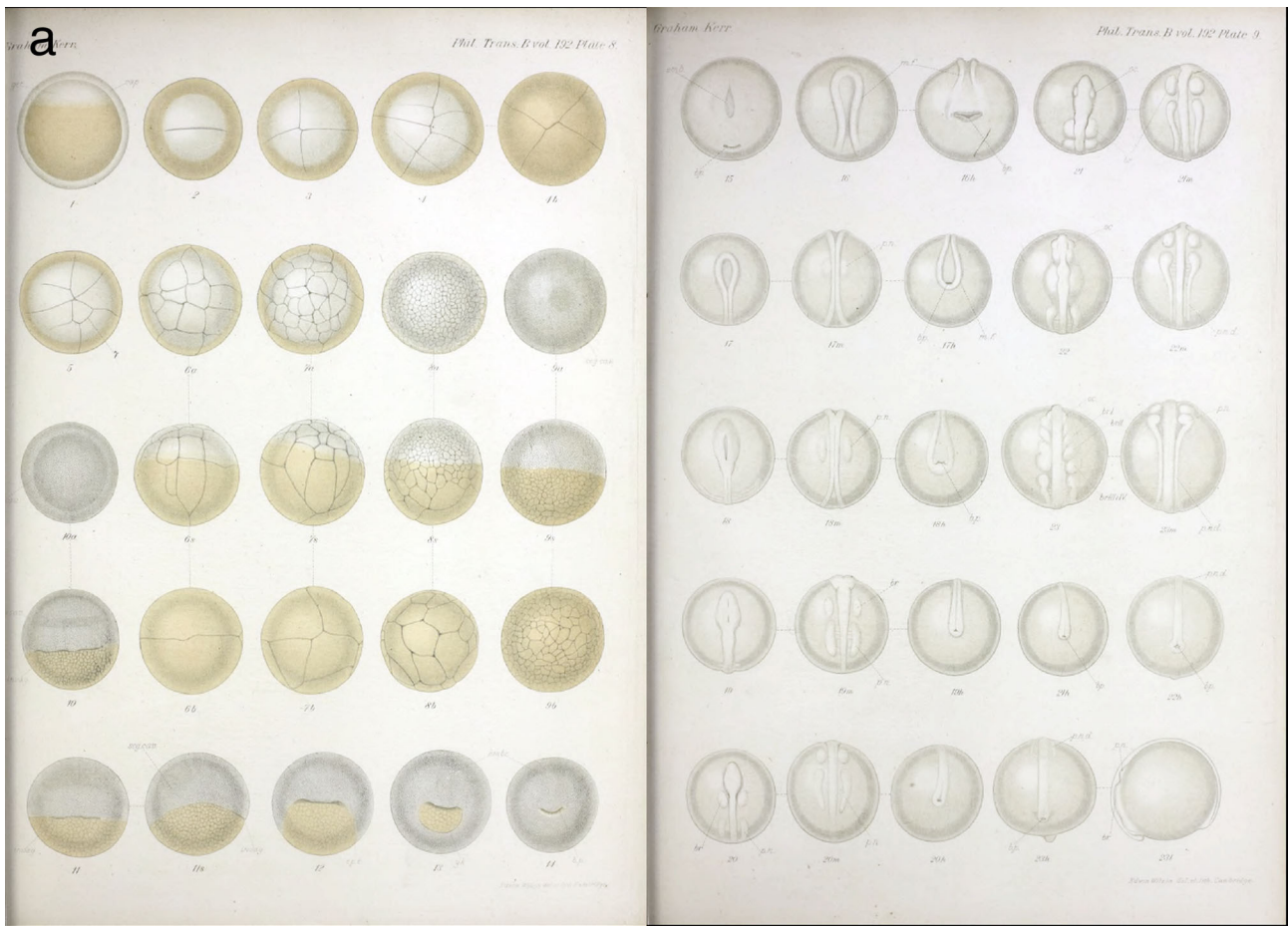
FIGURE 10   Legend on next page.

reconstruction of the ground pattern of the amniote egg. Menkhorst et al. (2009); Figure 5) recently summarized patterns of evolution of the mammalian egg. They highlighted that in comparison to the sauropsid/monotreme egg, which contained substantial quantities of yellow and white yolk (latebra), marsupials had lost most or all of the yellow yolk, lipid droplets, and yolk platelets, whereas the white yolk vesicles were retained to provide extracellular matrix. Finally, in eutherian mammals the white and yellow yolk were lost, except for some few lipid droplets in some species. Metatheria maintain an eggshell (Mossmann, 1987; Tyndale-Biscoe & Renfree, 1987), but it is lost in eutherian mammals (e.g., Ferner & Mess, 2011; Mossmann, 1987). Carter (2020) in this issue of the Journal of Morphology reviews the evolution of extraembryonic membranes in the major clades of mammals.

2.3.2 | Sauropsida

Eggs of oviparous sauropsids are commonly large relative to those of typical amphibians and actinopterygians. A thin vitelline membrane and a variable amount of albumen surround a large yolk ball. A leathery (i.e., collagenous) eggshell with calcium carbonate incrustations covers the egg externally; however, the eggshell structure is variable among sauropsids and hard shelled eggs have evolved in several lineages (Chelonia; Figure 15, Gekkota, Archosauria) in relation to nesting ecology (Kohring, 1995; review in D'Alba et al., ; this issue of the Journal of Morphology). Cleavage is meroblastic resulting in a blastodisc,

residing on the yolk ball. Laid eggs always contain an embryo, but the developmental stage depends on the duration of egg retention. Among squamates, viviparity evolved in numerous clades (at least 115 convergent origins; Blackburn, 2005, 2015a, 2015b). Studies on the structure and function of the laid egg are surprisingly rare and information about many details is missing.

2.3.3 | Chelonia

Upon egg laying, the yolk is structured into a central, liquid yolk and a peripheral yolk. To our knowledge and described only in *Trachemys scripta*, the yolk mass is structured in 14–15 alternating layers of white and yellow yolk spherically surrounding a center of white yolk that extends with a neck right under the germinal disk. The center is not well defined, but the stalk of white yolk extending under the germinal disk, that is, the latebra, is (Callebaut et al., 1997). Turtles possess a biomineralized eggshell with a radial aragonitic crystal structure; pore canals consist of widely separated simple tubes (i.e., "testudioid type"; Mikhailov, 1991, 1992; Grellet-Tinner et al., 2004; Gibbons et al., 2020). Turtles may have soft, flexible eggshells that are able to absorb water (Packard, 1980; Packard et al., 1979), or rigid eggshells (e.g., Kinosternidae [Packard, Hirsch & Iverson, 1984], *Apalone spinifera* [Packard & Packard, 1979], *Geochelone elephantopus* [Hirsch, 1983]). Kusuda et al. (2013) recognized six different types of eggshells with increasing complexity with up to 4 layers. Type VI of Kusuda et al. (2013) has three calcified

FIGURE 10 *Dipnoi*, cleavage and early embryogenesis in *Lepidosiren paradoxus* and *Neoceratodus forsteri*. **(A)** *Lepidosiren paradoxus*, plates 8 and 9 from Kerr (1900). Plate 8. All the figures on this plate were drawn under a magnification of eight diameters, and were reduced by the lithographer to 2/3 the size of the original drawing. The actual magnification in the figures is therefore slightly over five diameters (5 1/3). Where more than one figure of the same egg is given, *a* affixed to the number indicates view from above (i.e., from the animal pole aspect), *s* view from side and *b* view from below. (1) Unfertilized egg from coelomic cavity. (2) Egg showing first segmentation furrow. (3) Egg with two primary furrows, seen from above. (4) Egg after the appearance of the furrows of the third phase. (5) An egg of similar stage showing irregularity induced by one of the furrows of the third phase being latitudinal. (6–9) Illustrating the further progress of segmentation. In Figure 9a the segmentation cavity is indicated by a dark shadow. (10) Egg showing the commencement of invagination. (11) Slightly later stage seen from behind. In the side view the diminishing segmentation cavity is indicated by a shadow. (12–14) These figures illustrate the shortening up of the line of invagination, and the covering in of the yolk by the small superficial cells. Plate 9. Magnification as in Plate 8. The letters affixed to the numbers of the figures on this Plate signify: *h*, view from behind; *m*, view looking down on middle of trunk region of the embryo from the dorsal side; *l*, view from the side. (15) Egg slightly more advanced than that of (14). (16) Egg in which the medullary folds have appeared. (17) Egg in which the medullary folds have become closely apposed in the mid-trunk region, and showing the continuity of the medullary folds behind the blastopore. (18) Egg showing commencing fusion of the medullary folds. (19) Egg with the medullary folds nearly completely fused, and with first trace of the branchial eminence on each side. (20) Egg in which the fusion of the medullary folds is completed. (21) A somewhat later stage in which the optic outgrowths have appeared. (22) An egg in which the head fold of the embryo is beginning to develop. (23) Showing the segmentation of the branchial eminence, and the commencing development of the tail fold. Abbreviations: bp, blastopore, br, branchial eminence; br I, II branchial arches; cap, egg capsule; emb, depression over medullary plate; epc growing edge of epiblast; ger, germinal cap; invag, line of invagination; mf, medullary folds; oc, optic outgrowth from brain; pn, pronephros; pnd, pronephric duct; seg cav, segmentation cavity; yk, yolk cells. Original, reformatted caption from Kerr, J. G. (1900). The external features in the development of *Lepidosiren paradoxa*, Fitz. *Phil. Trans.*, B, 192, 299–330. Downloaded 24.07.2020 from philosophical transactions of the Royal Society B (https://doi.org/10.1098/rstb.1900.0005). (copyright in public domain). (b) *Neoceratodus forsteri*, normal series of divisions in early cleavage, stages 1–5. Camera lucida drawings from fixed specimens removed from the vitelline and albumen membranes. Figure 1 in Kemp (1982). (A) Stage 1, uncleaved egg. (B) Stage 2, first meridional cleavage. (C) Stage 3, second meridional cleavage at right angles to the first. (D) Stage 4, the third meridional cleavage, slightly irregular, with furrows on the convex surface lagging but usually dividing the cells from apex to base. (E) Stage 5, showing the first latitudinal cleavage, loss of the hemispherical shape as the segmentation cavity develops and delayed furrows in the convex surface. Scale line 1 cm. Original caption from Kemp, A. (1982). The embryological development of the Queensland lungfish, *Neoceratodus forsteri* (Krefft 1870). *Mm. Qd. Mus.* 20, 553–597. Downloaded 24.07.2020 from the Biodiversity Heritage Library https://www.biodiversitylibrary.org/page/52619118#page/185 (copyright CC-BY-NC-SA 4.0)
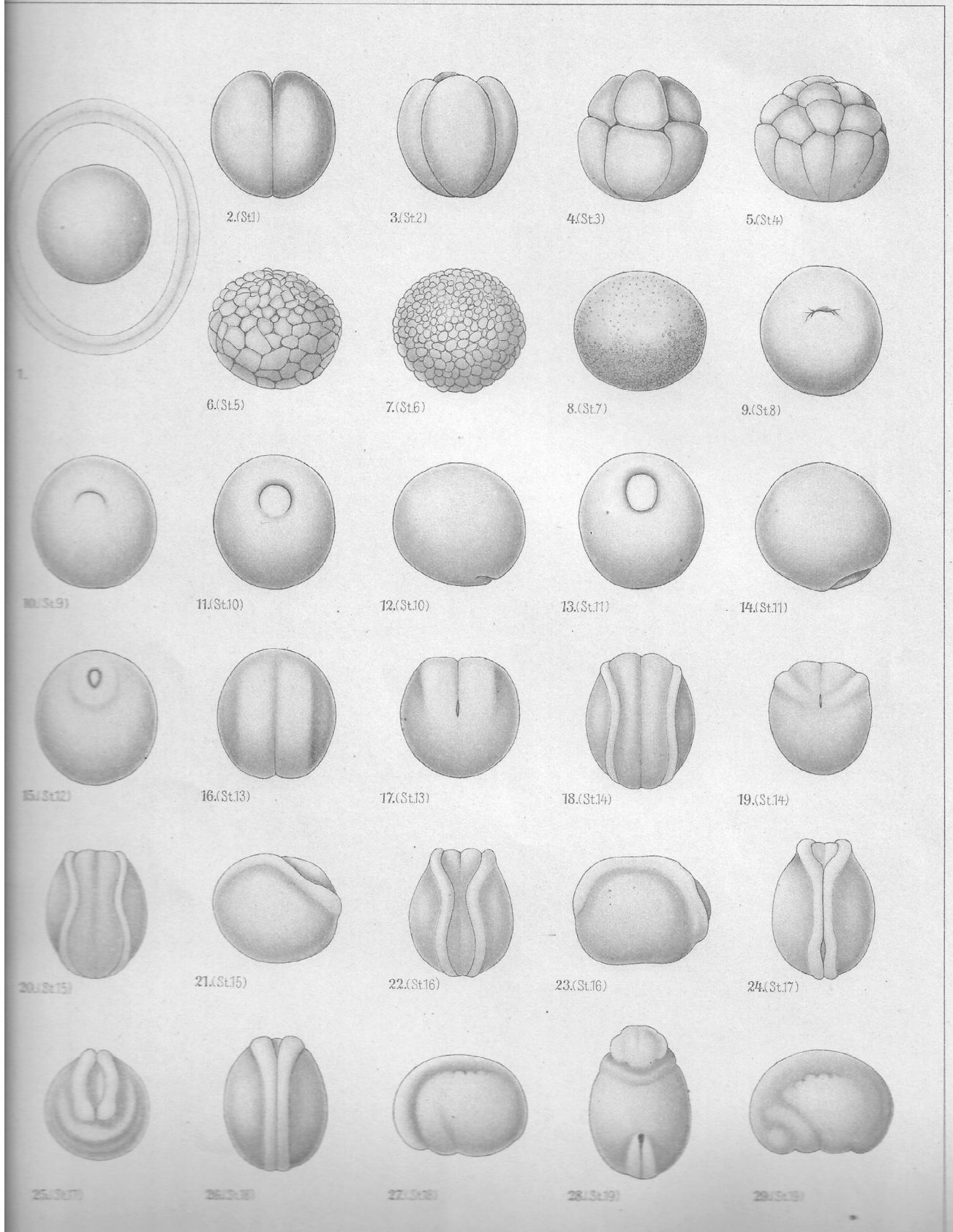
FIGURE 11 Legend on next page.

layers, and an external organic cortex that makes it similar to eggshells of birds. The similarity of the *Apalone* eggshell with avian eggshells was highlighted by Packard et al. (1979)—except for the aragonite crystallization of calcium carbonate in the turtle eggshell (e.g., Kusuda et al., 2013).

Yolk sac morphology and yolk uptake in Chelonia have received little attention historically. Agassiz (1857) described "a mesh of blood vessels covered by a sheath of yolk" (Figure 15) see: Elinson et al., 2014; Blackburn, 2020), but failed to recognize details of cellularization. Recent studies on *Chelydra serpentina* and *Trachemys scripta* (Blackburn, Lestz, Barnes, Appiah, & Bonneau, 2019; Blackburn, Lestz, Barnes, & Powers, 2019) have revealed a morphological pattern of cellularization of yolk and later association of cells with invading blood vessels that now appears to be typical for sauropsids, except birds (Blackburn, 2020). In these species, formation of the cellular yolk sac involves proliferation of endodermal cells that invade the yolk to phagocytose yolk material. Blood vessels only secondarily grow into the mass of endodermal cells that arrange around them (forming elongated "spaghetti-like" strands, as the authors call them, that fill the yolk sac cavity). These processes cellularize the yolk material and ultimately establish structures that supposedly function in uptake and transport of nutrients through the vitelline vessels to the developing embryo.

Little information is available on amnion and chorioallantois formation in turtles (Agassiz, 1857; Mitsukuri, 1891; Stewart, 1997). Rhythmic, myogenic amnion contractions have been described for various species of turtles (summarized in Turpaev & Nechaeva, 2000; Nechaeva, 2009). The chorioallantois functions as embryonic respiratory organ (Birchard & Reiber, 1993, 1995) and storage for excreta. The uptake of calcium from the eggshell through the chorioallantoic ectodermal cells has been shown for *Chelydra serpentina* and *Apalone spinifera* (Packard & Packard, 1991; Packard, Short, et al., 1984, Lawniczak & Teece, 2005).

2.3.4 | Sphenodon

Sphenodon punctatus is sister group to squamates and thus takes a crucial position in the phylogeny of sauropsids. However, because of its endangered status, descriptions of the egg and early embryogenesis are rare, most detailed (invasive) investigations date back to 19th and early 20th century. The tuatara has a semi-rigid eggshell with individual large mineralized units embedded in the external layer of the collagenous eggshell matrix. Structure and formation of the biomineralized eggshell are unique as compared with other sauropsids (Cree et al., 1996; Packard et al., 1988; Packard, Hirsch, & Meyer-Rochow, 1982). In the tuatara, the eggshell membrane is thick and externally covered by calcareous caps. Columns of calcitic calcium carbonate penetrate deeply into the shell membrane from the outer surface, and the surrounding fibers are embedded in these columns. In comparison, the calcareous layer of all other sauropsids is largely external to the shell membrane. The unique type of eggshell of the tuatara, suggests that it is a clade specific feature that differs from the more flexible eggshell as found in Chelonia and many squamates (Choi et al., 2018; Fernandez et al., 2015). However, tuatara females carry the eggs for 7–8 months in utero (Cree et al., 1992), and the eggshell is deposited slowly during that period. Thus, it is possible that the unusual structure of the eggshell is related to the reproductive physiology and adaptation to cold. It might also be a byproduct of the slow secretion of the eggshell. The eggshell of tuatara is a clade specific character. Because of the singularity of this character, we cannot give explanatory priority to phylogenetic, functional, or exaptive interpretations.

Dendy (1899) described the yolk and yolk sac of embryonic tuatara. He referred to the yolk as "usual yellow yolk" occupying almost the entire egg with little albumen surrounding it. However, his description of invasion of the yolk by blood vessels is of interest:

FIGURE 11 *Lissotriton vulgaris*, cleavage and early embryogenesis; plate 1 from Glaesner (1925). (1) Lateral view of a freshly laid egg with egg membranes. (2) Stage 1, lateral view, a very minor size difference is observed between the two blastomeres. (3) Stage 3 lateral view, four blastomeres of same size. (3) Stage 3, lateral view, four micromeres sit on top of the macromeres, cleavage furrows complete. (5) Stage 4, lateral view, 12 micromeres are distinctly separated from macromeres. Bilateral symmetry recognizable, longitudinal axis of the embryo in the orientation of the drawing. (6) Stage 5, lateral view, morula stage, upper hemisphere unequal, lower hemisphere smooth. (7) Stage 6, lateral view, blastula, upper hemisphere smoother than lower. (8) Stage 7, lateral view, individual blastomeres cannot be recognized anymore, embryo slightly elongate. (9) Stage 8, view onto blastopore. Blastopore is a somewhat irregular slit. (10) Stage 9, view onto blastopore. Blastopore is a distinct and clear slit. (11) Stage 10 view onto blastopore. Blastopore is oval, faint indication of the lower blastopore lip. (12) Same embryo as in 11, lateral view. (13) Stage 11, rear view, blastopore oval with a large yolk plug. (14) Same embryo as in 13, lateral view. (15) Stage 12, rear view, blastopore smaller than before, surrounded by inconspicuous swelling. (16) Stage 13, dorsal view, posterior end of embryo is to bottom of plate. Medullary plate with primitive groove. (17) Same embryo as in 16, blastopore is a narrow cleft, yolk plug almost disappeared. (18) Stage 14, dorsal view orientation like in 16. The medullary plate shows distinct medullary folds (Medullarwülste). (19) Same embryo as in 18, rear view, blastopore is a fine cleft between the ends of the medullary folds. (20) Stage 15, dorsal view, medullary folds are enlarged and approaching in the midline. (21) Same embryo as in 20, lateral view, embryo somewhat elongated in longitudinal axis. (22) Stage 16, dorsal view, medullary folds have approached in the midline, pear shaped body form. (23) Same embryo as in 22, lateral view, slight dorso-ventral flattening. (24) Stage 17, dorsal view; medullary folds meet in the dorsal midline. (25) Same embryo as in 24, anterior view, the rudiment of the head and pharyngeal region is clearly recognizable. (26) Stage 18 dorsal view, medullary folds have almost completely merged, posterior part of the brain recognizable, body shape elliptical. (27) Same embryo as in 26, lateral view, first somite(s) recognizable. (28) Stage 19, ventral view, rudiments of eyes and gills recognizable, anus is a small opening. (29) Same embryo as in 28, lateral view. Caption translated and edited by JMS from Glaesner, L. (1925). Normentafel zur Entwicklungsgeschichte des gemeinen Wassermolchs *(Molge vulgaris)*. In Normentafeln zur Entwicklungsgeschichte der Wirbeltiere, Vol 14. (Keibel, F., ed.) Gustav Fischer Verlag, Jena. pp. 1–49. (copyright in public domain)
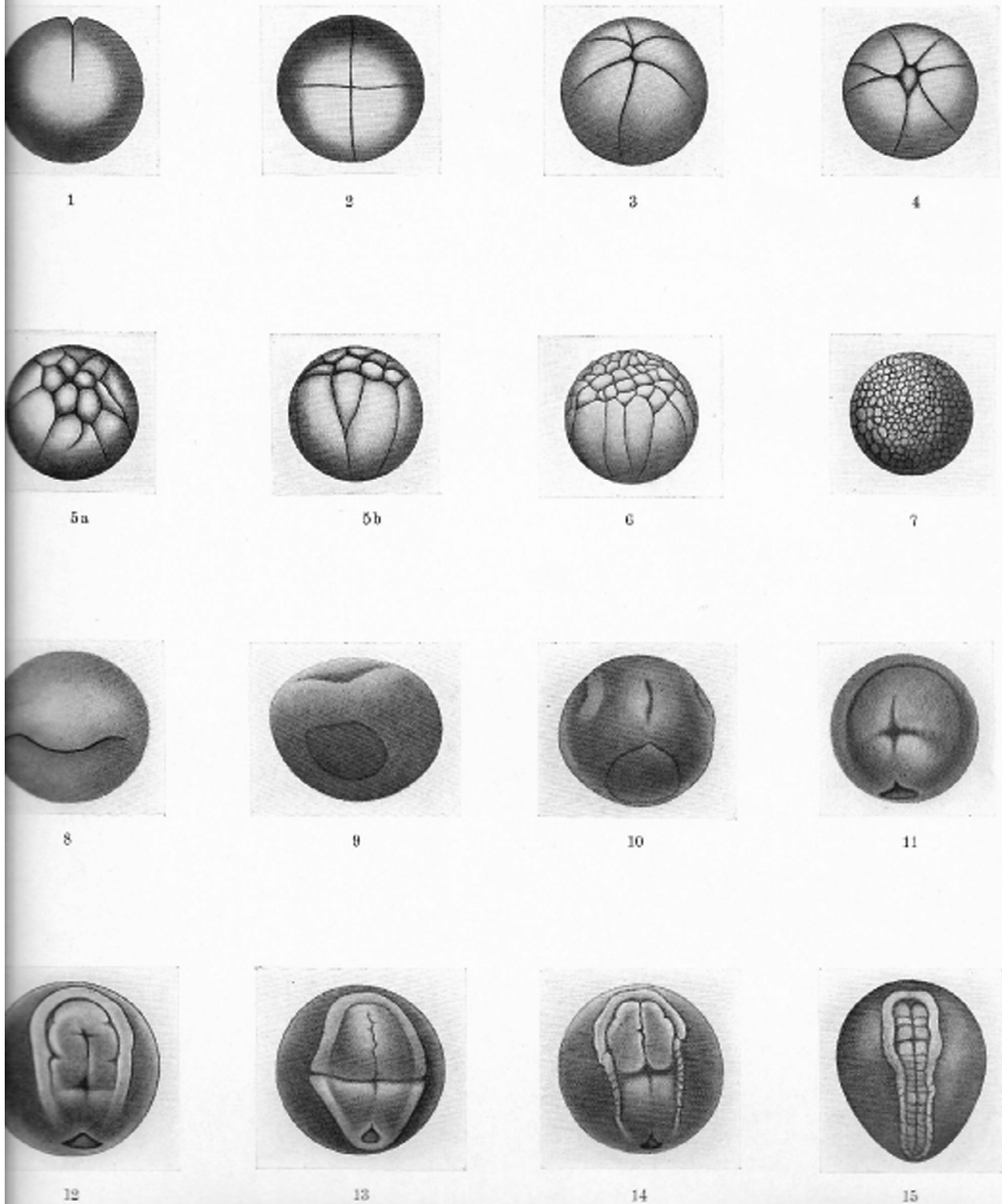
FIGURE 12 Legend on next page.

"*As development proceeds the absorbent blood-vessels dip into the yolk from the yolk-sac, and the large transparent spheres, each surrounded by a layer of crystalloids, become attached to these vessels like onions on a string. This ropy or radially columnar character of the yolk in the later stages of development is very striking even to the naked eye [...]*" (Dendy, 1899, p.13; figures 106, 107). Dendy's (1898) previous account revealed that he considered the large transparent spheres to be globules of yolk, whereas we now can infer that they probably are yolk-filled endodermal cells that adhere to invasive blood vessels (Blackburn, 2020), as described above in chelonians. Coupled with the accounts by Schauinsland (1899, 1903, for conflicts about priority and appropriate referencing, see Benham 1899), we can infer that free endodermal cells immigrate into the yolk, phagocytose yolk vesicles, and arrange in strands around blood vessels. Despite missing details of cellularization and vascularization of the yolk, these early accounts are remarkable because their descriptions recognized basic elements of the structural and developmental features which have now been summarized for other sauropsid clades in much greater detail (except birds) by Blackburn (2020, this issue of the Journal of Morphology.).

2.3.5 | Squamata

An outstanding diversity of reproductive modes exists among squamates (e.g., Blackburn, 2015a, 2020; Stewart & Thompson, 2017). This diversity of reproductive modes evolved from an oviparous ancestor through multiple evolutionary origins of various forms of egg retention and viviparity (e.g., Blackburn, 1982, 1985; Blackburn et al., 2003; Blackburn & Flemming, 2009; Hughes & Blackburn, 2020; Stewart, 2013; Stewart, 2020). Morphological variation concerns almost all aspects of the squamate egg, that is, eggshell, shell membranes, yolk and extraembryonic membranes. Complete reduction of the eggshell in species with viviparity (e.g., Blackburn, 1982, 1985, 2005), or the independent evolution of hard shelled eggs (in Gekkota; analogous to turtles and archosaurs; Bustard, 1968; Kratochvíl & Frynta, 2006; Choi et al., 2018; Pike et al., 2012) represent contrasting conditions of that morphological diversity. Not surprisingly, Hallmann and Griebeler (2015) found strong phylogenetic signal in the egg shell structure of squamates at low taxonomic levels and an association with different life history traits (Hallmann & Griebeler, 2015), that is, the egg shell in squamates was frequently modified in association with life history and reproduction (review: D'Alba et al., 2021). Here, we focus on the supposedly ancestral egg of squamates, but do not discuss evolutionary modification among clades of squamates.

Most probably, the ground pattern of eggshell structure was a flexible collagenous eggshell that contained calcitic cores of biomineralization. According to Packard and DeMarco (1991), the mineralized layer of most squamate eggshells is not embedded in the fibrous membrane but sits on top of the membrane. Eggs of oviparous Lepidosauria have only a single shell membrane (in contrast to Chelonia, Crocodylia and Aves), upon which relatively small amounts of calcium carbonate are deposited. Mammillary cores as centers of crystallization are absent (Kusuda et al., 2013). A remarkable variation in eggshell structure has been reported recently in the teiid lizard, *Salvator merianae*, which requires mention because it departs dramatically from all other sauropsids (Campos-Casal et al., 2020). In contrast to other sauropsids, the biomineral component of the shell is hydroxyapatite and, unlike other squamates, calcium is embedded deep in the fibrous matrix of the eggshell. The significance of this derived morphology is as yet unknown. The soft and flexible egg of squamates shares with *Sphenodon* eggs and turtle eggs the ability of turgescent swelling to absorb water from the environment (Lillywhite & Ackermann, 1984; Packard & Packard, 1980; Seymour & Ackerman, 1980; Thompson, 1987). The organization of the eggshell into a series of troughs and crests might serve to increase the surface area available for contact with the substrate and to increase the capacity of the eggshell to stretch as the egg absorbs water (Packard, Burns, et al., 1982). Of course, the (flexible) calcareous layer of squamate eggs may also provide a protective function, mechanical as well as a barrier to microorganisms.

Contrary to occasional claims (Packard et al., 1977), albumen reportedly is absent from squamate eggs (Blackburn, 1998; Giersberg, 1922; Girling, 2002; Siegel et al., 2011; Siegel et al., 2015). The yolk is deposited as yellow and white yolk. A latebra has been described for *Lacerta agilis* (Sarasin, 1883) and later confirmed by Boyd (1940) for *Hoplodactylus maculatus* and *Lacerta agilis*. No other reports were found in the literature; thus, it remains unclear if a latebra is absent or has just not been mentioned. The cellular yolk sac, and the morphological structures involved in uptake of yolk resemble

---

FIGURE 12 *Andrias japonicas*, cleavage and early embryogenesis (plate 1 from Kudo, 1938). (1) Stage 1, lateral view, diameter 5.6 mm, first cleavage reaches to the equator, both blastomeres of about same size. Stage 2, dorsal view, second cleavage, egg diameter 5.3 mm. (3) Stage 3, dorso-lateral view, 6 unequal blastomeres. (4) Stage 4, dorsal view, 8 unequal blastomeres. (5a) Stage 5, dorsal view, 7 micromeres for a cap on the 7 macromeres. (5b) Same egg as (5a) lateral view. (6) Stage 6, lateral view 36 micromeres and 16 macromeres. (7) Stage 7, dorsal view, blastula, ∼275 micromeres and 25 macromeres. (8) Stage 8, view onto the blastopore, embryo slightly elongated, the blastopore is a slightly convex line. (9) Stage 9, view onto the blastopore; the blastopore forms a ring that embraces the yolk plug. (10) Stage 10, dorso-caudal view blastopore lowered in position, still very large, primitive groove and neural folds are recognizable. (11) Stage 11, dorsal view, blastopore reduced in size, the primitive groove is crossed by the sulcus myelo-encephalicus. (12) Stage 12, dorsal view, blastopore has the shape of a triangle, medullary folds distinct. (13) Stage 13, dorsal view, blastopore reduced, the sulcus myelo-encephalicus distinct. (14) Stage 14, dorsal view, medullary folds approach the midline. (15) Stage 15, dorsal view, the embryo is elongated, the blastopore is recognizable as a narrow cleft. Numerous neuromeres are present. Caption translated from original German (shortened and edited) by JMS from Kudo, T. (1938). Normentafeln zur Entwicklungsgeschichte des Japanischen Riesensalamanders *(Megalobatrachus japonicus* Temmink). Normentafeln zur Entwicklungsgeschichte der Wirbeltiere, Vol 16 (Keibel, F. Ed.). Verlag Gustav Fischer, Jena. pp. 1–49
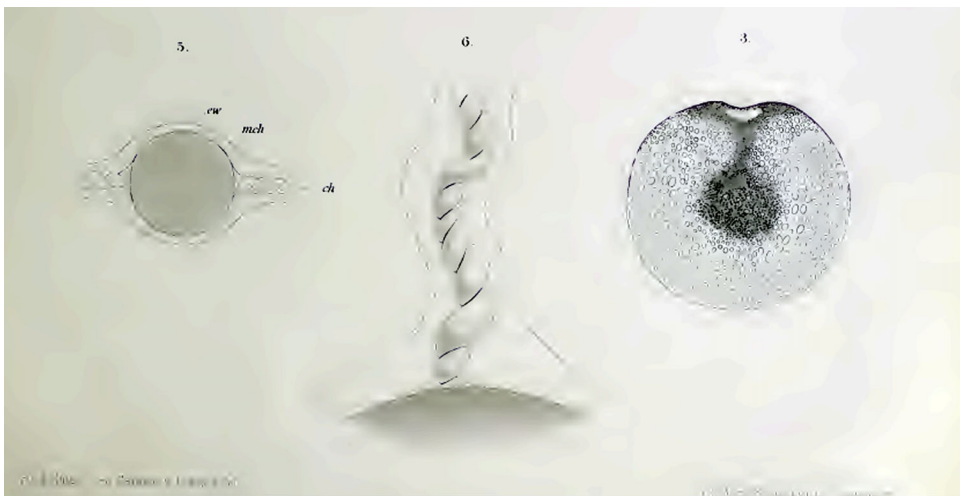
FIGURE 13 *Ichthyophis glutinosus*: Egg and early embryogenesis; plate 1 (Figures 3, 5, 6) and plate 3 from Sarasin and Sarasin (1887). (3) Cross section through a ripe ovarial egg. (5) Egg membranes with chalazae. (6) Detail of one egg pole with a chalaza. (19) schematic longitudinal section through an embryo (from Figure 17) and yolk. (20) Part of the yolk from same series. (21) Slightly later stage of embryo. (22) Head of the embryo in lateral view. (23) Prosencephalon with olfactory pits in ventral view. (24) Same head with otic vesicles, seen from above. (25–28) Heads of various embryos. (29) Section through a blastodisc at the end of cleavage process. Caption translated from original German text by JMS from Sarasin, P., & Sarasin, F. (1887). Zur Entwicklungsgeschichte und Anatomie der Ceylonesischen Blindwühle *Ichthyophis glutinosus*. CW Kreidel. Downloaded 13.02.2021 from https://www.zobodat.at/pdf/MON-V-HERP_0023_0001-0263.pdf (copyright expired, now public domain)
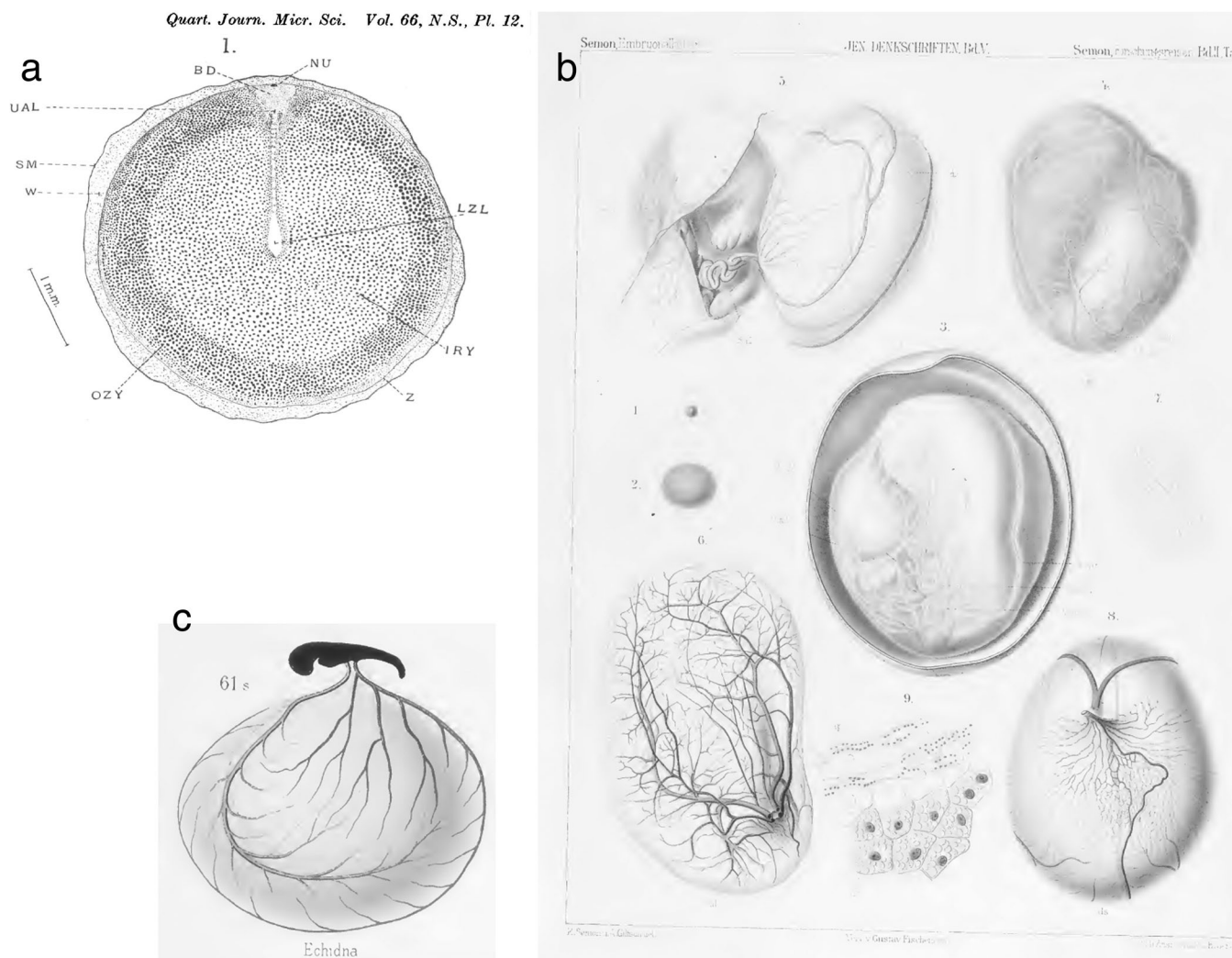
FIGURE 14 *Monotremata*, egg and various embryonic stages. (a) *Ornithorynchus paradoxus*, fully-formed egg of *Ornithorhynchus paradoxus*, in vertical section. Shows latebra, yolk, albumen, and shell-membrane (plate 12, figure 1 in Gatenby (1922). Downloaded 29.07.2020 from Journal of Cell Science. Gatenby, J. B. (1922). Memoirs: Some notes on the gametogenesis of *Ornithorhynchus paradoxus*. *Journal of Cell Science*, 2(263), 475–496. (copyright for reuse of figure grated by the Company of Biologists, # 1099126; 22.02.2021) (b) *Echidna aculeata*, egg and various embryonic stage with yolk sac circulation (plate 1, figures 1–9 in Semon, 1894). (1) Egg from uterus, removed from egg shell. (2) Egg from marsupium (3) Same egg after opening of egg shell, seen from allantoic side. (4) Same sample after complete removal of the egg shell. (5) same embryo after removal of membranes and repositioning of the yolk sac. (6) Allantoins of same embryo seen from stalk. (7) Vascularization network of the allantois on the side of the stalk, where it is not merged with serous membranes. (8) Yolk sac of same embryo seen from stalk. (9) Epithelium of the yolk sac seen from the lumen with capillaries reaching around the epithelial cells. (c) Plate 7, figure 61 from Semon (1894). Schematic drawing of the yolk sac circulation of *Echidna*. Downloaded 27.08.2020 https://www.zobodat.at/pdf/Denkschr-Med-Natwiss-Ges-Jena_5_1_0017-0058.pdf. Semon, R. (1894). Die Embryonalhüllen der Monotremen und Marsupialier. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena*, 5, 19–58. (copyright in public domain)

that found in turtles and the tuatara (see description above), that is, cells of the extraembryonic endoderm immigrate into the yolk and cellularize it. They later associate with blood vessels that grow into the yolk and, together, provide a nutritive structure. This pattern of yolk absorption has now been described in all sauropsid clades except birds, in which it is lacking (e.g., Elinson & Stewart, 2014; Powers & Blackburn, 2017; Blackburn et al., 2018; Blackburn et al., 2019, b; Blackburn et al., 2020; review in Blackburn, 2020, this issue of the Journal of Morphology), and thus is considered a symplesiomorphy that squamates share with all other sauropsids.

During embryonic development, the cellular yolk sac grows around the yolk mass. However, as a unique character of squamates, the extraembryonic mesoderm grows into the yolk forming the yolk cleft (part of the extraembryonic coelom). This process isolates a thin segment of yolk (i.e., the "isolated yolk mass") from the main body of the yolk (e.g., figure 1 in Stewart, 2020; this issue of the Journal of Morphology). The yolk cleft and the isolated yolk mass have been described in more than 65 squamate species in 12 families (e.g., Blackburn & Stewart, 2011; Stewart, 1985, 1990, 1993; Stewart et al., 2012; Stewart & Blackburn, 2019; Stewart & Florian Jr., 2000; Stewart & Thompson, 2017). The functional implications
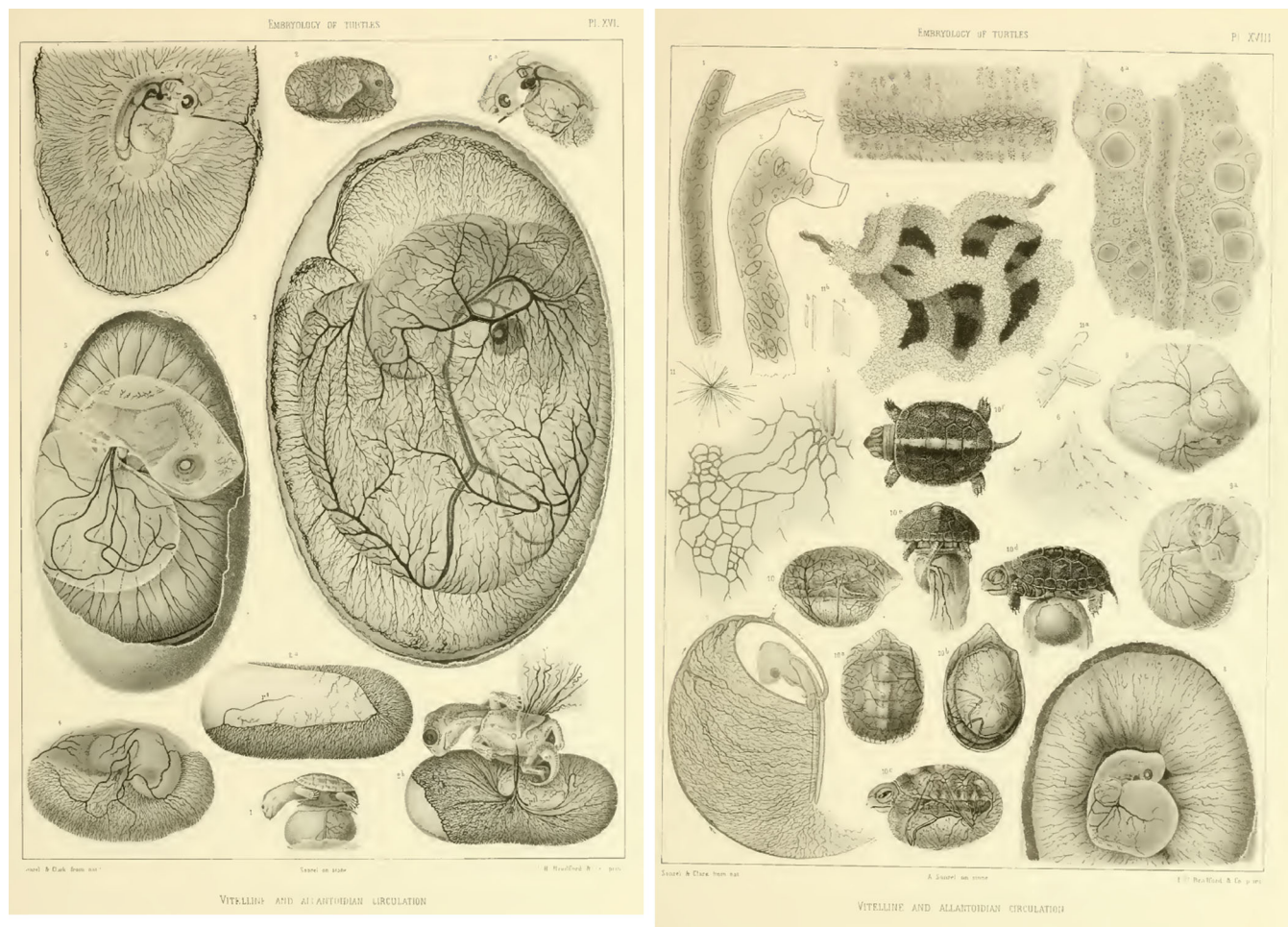
FIGURE 15 Chelonia, yolk sac and chorioallantois of late embryos. (a) Plate 18 from Agassiz (1857). *Chrysemys picta*. (1) The allantois and amnion removed. Nat size. Laid June 21, opened Oct. 23, 1855. (2) From above, the shell cut away, nat. Size. (2a) the same as (2), from below, about 2 diam., the shell being removed to show the superficial extent of the vascular area; r^1, vena afferens. (2b) the same as (2), and (2a), the allantois and amnion cut away, and the embryo turned back and exposed from below; r^1, the point where the vena afferens enters the yolk mass. Laid June 21, opened Sept. 1, 1855. (3) From above, 5 diam.; r^1, vena afferens. Laid June 16, opened Aug. 1, 1855. (4) seen obliquely from above and to the right, about 2 diam. Period of laying unknown, opened Sept. 17, 1852. (5) From above, a little more than 3 diam. The allantois is drawn back. Date of laying unknown, opened Aug. 2, 1855. (6) *Nanemys guttata*, from above and to the right. (6a) The same from the left, without the vascular area; about 4 diam. Laid June 20, opened July 17, 1855. **(B)** Plate 18 from Agassiz (1857). (1) Omphalo-meseraic vein with a very thick wall, 500 diam.; the same as Pl. 1 7, Figures 3, and 7. *Ch. serpentina*. (2) Omphalo-meseraic artery, 500 diam. Embryo just hatched. (3) Piece of the allantois with a bloodvessel, 500 diam. Period of laying unknown, opened Aug. 27, 1852. (4) Mesh of bloodvessels covered by yolk. 20 diam. (4a) A single vessel in its sheath of yolk, 500 diam. *Ch. serpentina*. Just hatched. (5) Posterior end of the dorsal artery and the neighboring omphalo-meseraic arteries. Magnified from (7) *Nanemys guttata*. Laid July 11, opened July 22, 1852. (6) The fork of the vena terminalis, 12 diam.; the same as (7). (7) From below, 5 diam.; the same as (5) and (6). (8) From above, 3.5 diam. *Nanemys guttata*. Period of laying unknown, opened Aug. 21, 1852. (9) From above, 2 diam. *Ozotheca odorata*. Period of laying unknown, opened Aug. 23, 1852; (9a) The same as (9). The embryo and allantois drawn to one side. (10) From the right side; (10a), from above. (10b) From below; (10c) from the left side, the allantois partly opened; (10d), the same, the allantois being cut away. (10e) The same, from behind; (10f) same as (10d, 10e), from above. *Cistudo virginea*, nat. size. Just ready to hatch. Period of laying unknown. (10, 10b, 10c), opened Aug. 31, 1855; (10a, 10d, 10e,10f, opened Sept. 5, 1855.(11, 11a, 11b) a, b Crystals of nitrate of lime. See p. 508, on the structure of the egg-shell. original caption from Agassiz, L. (1857). Contributions to the Natural History of the United States of America, First Monograph, Volume II, Part III—Embryology of the turtle. Little, Brown and Co., Boston. (copyright in public domain)

of this structure are unknown. However, it gives rise to the formation of a yolk sac placenta in some viviparous species.

The chorioallantois of oviparous squamates is an intensively vascularized transitory embryonic exchange organ (e.g., Birchard & Reiber, 1993, 1995). During development, the chorionic epithelium flattens, thus reducing the diffusion barrier through the eggshell, chorionic epithelium and capillary wall (Kim & Blackburn, 2015, 2016). However, the capillaries remain sandwiched between the epithelia of chorion and allantois and do not integrate into the chorion or the shell membrane as they do in birds (see below). Morphological and physiological studies reveal that the chorioallantois provides nutritional support for the embryo by mobilizing calcium from the eggshell (Blackburn et al., 2003;

Ecay et al., 2004; Jee et al., 2016; Packard & Packard, 1984; Packard, Short, et al., 1984; Stewart et al., 2004). This function has been documented in all oviparous sauropsids that have been studied (Packard, 1994) and may be an ancestral function of the chorioallantois (irrespective of the phylogenetic position of turtles).

2.3.6 | Crocodylia

The eggshell is rigid and three- (Ferguson, 1982) or two-layered (crocodyloid type: Ferguson, 1982; Mikhailov, 1992, 1997; Marzola et al., 2015). Pore canals reach from the surface to the mammillary layer (Ferguson, 1982; Wink et al., 1990). Internally, two eggshell membranes (Packard et al., 1977; Rathke, 1866) cover it. Whether or not an air cell forms during incubation between the two membranes remains unclear. The eggshell is the primary source of calcium for the developing embryo (Packard & Packard, 1989; Packard & Seymour, 1997). The eggs do exchange water with the environment (uptake and loss) although this may be a response to extreme incubation conditions (Packard & Packard, 1988).

Surprisingly little published information was found on the albumen and yolk structure, as well as extraembryonic membranes of crocodiles. As in all other vertebrates (Nelsen, 1953), an acellular vitelline membrane surrounds the freshly deposited yolk (Reese, 1908). Voeltzkow (1901) provided an interesting and important account on the cellular yolk sac of *Crocodylus niloticus*: "[...] *Es verzweigen sich nicht nur die Gefäfse auf der Oberfläche des Dotters, sondern sie entsenden auch feine Fortsätze in den Dotter selbst hinein. Die ersten Anfänge davon sind in figure 36 auf Taf. XXXV dargestellt. Diese Fortsätze dringen central gerichtet von allen Seiten mehr und mehr, tiefer und tiefer in den Dotter ein, dabei an der Basis an Stärke zunehmend und sich vielfach verästelnd und verzweigend und sich schliefslich in ein System so feiner Kapillaren auflösend, dafs der ganze Dotter von ihnen durchsponnen ist und eine völlig verfilzte Masse darstellt.*" [...][1] (Voeltzkow, 1901, p. 362). This and the recent study by Blackburn et al. (2020) on *Alligator mississippiensis*, are the only accounts on the cellular yolk sac structure. Despite being almost 120 years apart and on two different species, these two studies explicitly document the ancestral pattern of yolk sac structure as described above for other sauropsids.

Besides general knowledge of the large volume of the albumen, we know little to nothing about its structure. This is particularly important because Crocodylia and birds are extant sister taxa of archosaurs, and because birds (see below) show structural features of the albumen not known from other sauropsids, that is, the chalazae. However, we found explicit statements by Rathke (1866, p. 7 §3), Reese (1908), p. 5) and Ferguson (1982) that chalazae are not present in Crocodylia, as in all other non-avian sauropsids.

The chorioallantois of crocodiles has not been studied in (histological/functional) detail (Stewart, 1997). However, numerous reports exist (e.g., Augustine & Watkins, 2015; Ferguson, 1982; Iungman et al., 2008; Webb et al., 1987) that the developing chorioallantois forms a ring band internal to the eggshell. To the end of incubation, the chorioallantois covers the entire inner surface of the egg. The formation of the opaque band of the chorioallantois characterizes crocodiles; a functional or developmental explanation is missing. We have not found published information about the amnion of crocodiles, except a general reference to myogenic contractions of the amnion (Nechaeva, 2009).

2.3.7 | Aves

Despite its paradigmatic bearing and standard example as "the amniote egg," the avian (Neornithes) egg has many unique features not shared with any of the other amniote clades. Many of those relate to elevated metabolic rates, thermally regulated incubation, parental attendance, and comparatively fast embryonic growth (Ricklefs & Starck, 1998; Starck, 1989, 1993, 1999, 2018; Starck & Ricklefs, 1998).

Egg shape (Deeming & Ruta, 2014) of birds (Aves; Figure 16) differs from that of their theropod ancestors and other sauropsids in the degree of asymmetry, that is, a feature not present in their sauropsid relatives. Because of the continuous distribution of this quantitative character in morphospace (Stoddard et al., 2017, 2019), and because of the observed variation of this trait among sauropsids, egg asymmetry is difficult to grasp as a distinct phylogenetic character. Thus, we have only tentatively included it into our character matrix.

Eggshell: Birds possess a rigid multilayered, biomineralized eggshell. It is three-layered with (a) an *outer cuticle* (domestic chicken, ~10 μm, organic layer, proteoglycans), (b) a *biomineralized layer* (domestic chicken, ~300 μm) and (c) the *outer* (domestic chicken, ~50 μm) and *inner* (domestic chicken, ~20 μm) *shell membranes* (collagen fibers). Avian egg shell thickness varies depending of egg mass and phylogenetic relationship (e.g., Rahn & Paganelli, 1989) as well as other life history parameters such as incubator mass and clutch size (Birchard & Deeming, 2009). The outer cuticle is a thin organic layer that may also carry pigments of egg coloration and has antimicrobial properties (e.g., Hincke et al., 2008, 2012). The biomineralized layer is highly structured. Its basic unit is the *eisosphrite*, an inorganic crystallization center that inserts in the outer shell membrane. Calciferous, calcitic cones grow radially away from the eisosphrite. Outside to the cone layer (syn. *mammillary layer*, *calcium reserve assembly*), the calcium crystals form a columnar layer (*palisade layer*) which constitutes the thickest layer of the biomineralized eggshell. The calciferous cones emerging from one eisosphrite, the mammillary layer, and the associated column layer form a basic unit of the eggshell. Outside to the column layer is an external zone of irregular arrangement with no crystallized structure (*vertical matrix layer*). Pore canals penetrate the biomineralized eggshell between the palisades. The pore canals are an important functional feature of the egg, because they provide the structures of gas exchange for the developing embryo. A remarkable diversity of eggshell pore shapes and numbers exists within and among species. Simple pores may be straight tubes or funnel shaped with the large opening to the outside, but more complex branching patterns have been described too (Maina, 2017; Riley et al., 2014; Willoughby et al., 2016). This eggshell morphology builds upon the
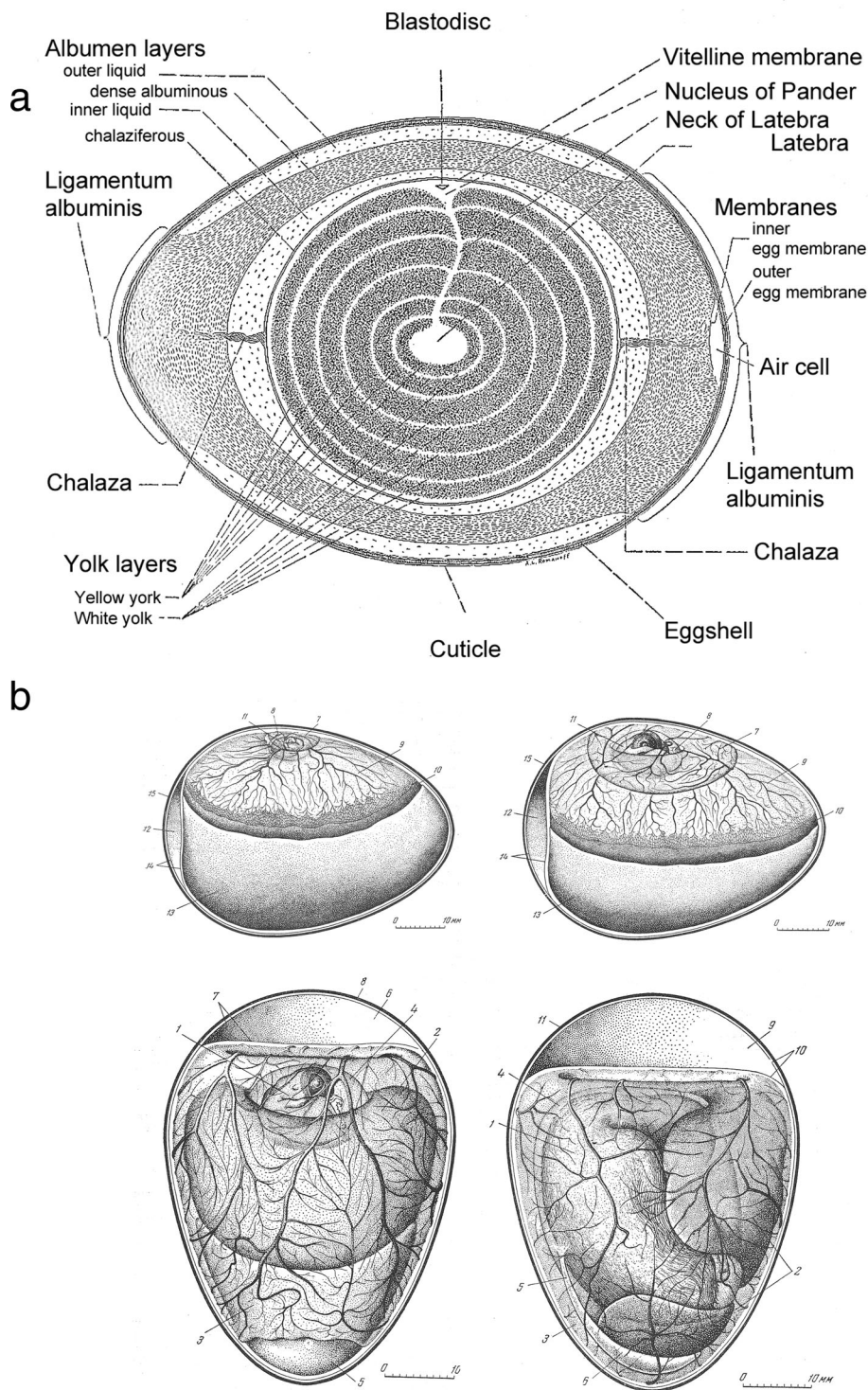
FIGURE 16 Avian egg and embryos. (a) Schematic drawing of a longitudinal section through an avian egg showing relevant morphological features. Redrawn from Romanoff, A. L., & Romanoff, A. J. (1949). The avian egg. John Wiley and Sons, Inc., New York, NY (no living person/institution known to claim copyright; extensive search documentation). (b) Avian embryos, *Gallus gallus* f. dom. At consecutive stages of development documenting the development of the yolk sac and the chorioallantois. (1), after 4 days of incubation, the yolk sac membrane has grown half way over the yolk and develops a dense vascular network; the chorioallantois is just a very small rudiment. (2) After 6 days of incubation, the chorioallantois has increased in size and major chorioallantoic vessels are recognizable. (3) After 10 days of incubation, the chorioallantois has reached maximum size extending over the entire inner surface of the eggshell. The chorioallantois functions now as the respiratory exchange organ of the embryo. The yolk sac membrane fully encloses the yolk sac (4) After 18 days of incubation; no further morphological changes of the chorioallantois. The embryo is a few days before hatching. Abbreviations: 1, embryo; 2, amnion; 3, allantois; 4, yolk sac membrane; 5, extraembryonic endoderm; 6, albumen; 7, eggshell membrane; 8, air space, 9, biomineralized eggshell; 10, chorioallantois membrane; 11, blood vessel in the chorioallantois membrane; 12, blood vessel in the yolk sac membrane. Scale bar, 10 mm; redrawn from Raginosa, M. N. (1961). Embryonic development of domestic chick and its relationship to yolk and extraembryonic membranes. Moscow, Russia: Academy of Sciences. 131 pp. (in Russian). (No living person/institution known to claim copyright; extensive search documentation)

pattern observed in other sauropsids. However, the degree of differentiation is so advanced that we consider it apomorphic, because it is not found in any of the other sauropsids. The eggshell is not only mechanical protection, but also has important biocidal functions and the mammillary layer of the biomineralized component serves as calcium depot for the developing embryo (Coleman & Terepka, 1972; Gabrielli, 2004; Österström & Lilja, 2012).

Inner and outer shell membrane separate during the development and form an air cell. The air cell primarily compensates for volume changes of the egg content due to water loss. At the end of the incubation period, when the term embryo starts aerating the lungs, it serves as a respiratory chamber. The air space of avian eggs is unique and therefore considered apomorphic. Based on the topology of the sauropsid phylogeny, a similar air space in turtles (Packard & Packard, 1979) is probably a convergent evolutionary development. It is unclear if the air space simply develops as a by-product ("spandrel"; Gould & Lewontin, 1979) of volume changes in the egg, or if it is genetically programmed.

TABLE 1 Character matrix (empty fields indicate no data available)

#	Character	Petromyzontidae	Myxinidae	Chondrichthyes	Polypterus	Acipenser	Lepisosteus	Amia	Teleostei	Latimeria	Dipnoi	Amphibia	Monotremata	Marsupialia	Euplacentalia	Testudines	Rhynchocephalia	Squamata	Crocodylia	Aves
1	Developmental stage at oviposition	0	0	?	0	0	0	0	0/1/2/3[a]	0	0	0/1/2/3	2	3	3	2	2	2	2	2
2	Vitelline membrane	1[b]	1	1	1	1	1	1	1	1	1	1	1	?	0[c]	1	1	1	1	1
3	Cleavage	1	2	2	1	1	2	1	1/2	?	1	1/2	1	1	1	2	2	2	2	2
4	Jelly coat	0				1[d]					1/0[e]	1	0	0	0	0	0	0	0	0
5	Fertilization	1	1	2[f]	1	1	1	1	1/2	2	1[g]	1/2	2	2	2	2	2	2	2	2
6	Copulatory organ (s)	0	0	1	0	0	0	0	0/2[h]	0[i]	0[j]	0/3[k]	4	4	4	4	4[l]	4[m]	4	4[n]
7	Embryonic excretory product[o]	1	1	2	1	1	1	1	1	1	1	1	3	2	2	3	3	3	3	3
8	Amnion	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
9	Chorion	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
10	Allantois	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
11	Absence of larva	0	?	1	0	?	?	0	0/1	1	0	0/1	1	1	1	1	1	1	1	1
12	White yolk	1[p]	1[p]	1[p]							0	0/1[p]	1	0	0	1	1	1	1	1
13	Latebra										0	0/1[p]	1	0	0	1	1	1/0[q]	1	1
14	Cellular yolk sac	1	1	2	0	3	3	0	3	0	0	0	4	6[r]	6[s]	5[t]	5[u]	5/6[v]	5[w]	7[x]
15	Egg shell	1	1	2	0	0	0	0	0	0	0	0	0	0	0	3	3	3	3	3
16	Myogenic contractions of amnion	0	0	0	0	0	0	0	0	1	0	0	?	0	0	1	1	1	1	1
17	Yolk	1	3	3	1	2	2	2	1/2	1	2	2	4	4	4	3	3	3	3	3
18	Chorioallantois	0	0	0	0	0	0	0	0	0	0	0	2	0/1	1	2	2	1/2	2	2
19	Egg shell as calcium depot	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
20	Egg absorbs water from environment	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
21	Egg shell membrane layers	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	2	2	2
22	Crystal structure	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	2	2
23	Albumen	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0[y]	0[y]	1	1

(Continues)

TABLE 1 (Continued)

#	Character	Petromyzontidae	Myxinidae	Chondrichthyes	Polypterus	Acipenser	Lepisosteus	Amia	Teleostei	Latimeria	Dipnoi	Amphibia	Monotremata	Marsupialia	Euplacentalia	Testudines	Rhynchocephalia	Squamata	Crocodylia	Aves
24	Organic core at base of shell unit	0	0	0	0	0	0	0	0	0	0	?	?	?	0	1	2	1	1	1
25	Egg shell pore canals	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
26	Isolated yolk mass	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
27	Opaque band of CAM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
28	Yolk absorption	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	2	2	2	3
29	Biomineralized egg shell layers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1/4	2	1	3	4
30	Hematopoietic tissue	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
31	Nucleus of Pander	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
32	Air cell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1
33	Egg asymmetry	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
34	Capillaries of CAM in shell membrane	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
35	Chalazae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
36	Yolk in multiple organized layers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
37	Organic cuticle external to egg shell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0	0	0	1
38	Eggshell pigmentation	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
39	Egg turning	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
40	Reproduction	0	0	0	0	0	0	0	0/1	0	0	0/1	1	1	1	1	1	1	1	1

Character	Character state
1 Developmental stage at oviposition	0 = unfertilized, 1 blastula, 2 = Embryo, 3 = viviparity
2 Vitelline membrane	present in all => no phylogenetic value
3 Cleavage	1 = holoblastic, 2 meroblastic
4 Jelly coat	0 = absent; 1 = simple jelly coat
5 Fertilization	1 = external, 2 = internal
6 Copulatory organ	0 = absent, 1 = claspers, 2 = gonopod, 3 = Amphibian, 4 = midline intromittent organ

TABLE 1 (Continued)

#	Character	States
7	Embryonic excretory product	1 = ammonia, 2 = urea, 3 = uric acid
8	Amnion	0 = absent, 1 = present
9	Chorion	0 = absent, 1 = present
10	Allantois	0 = absent, 1 = present
11	Loss of larva	0 = absent, 1 = present
12	White yolk	0 = absent, 1 = present
13	Latebra	0 = absent, 1 = present
14	Cellular yolk sac	0 = absent, 1 = Myxine, 2 = Chondrichthyes, 3 = teleost (yolk syncytial layer), 4 = amniote, 5 = spaghetti strands, 6 = placenta, 7 = avian
15	Egg shell	0 = no egg shell, 1 = collagenous, 2 = capsule (leathery), 3 = biomineralized
16	Myogenic contraction of amnion	0 = absent, 1 = present
17	Yolk	1 = polylecithal, 2 = oligolecithal, 3 = megalecithal, 4 - alecithal
18	Chorioallantois	0 = absent, 1 = feto-maternal exchange organ; 2 = respiratory organ
19	Egg shell as calcium depot	0 = absent, 1 = present
20	Egg absorbs water from environment	0 = absent, 1 = present
21	Egg shell membrane shell layers	1 = 1, 2 = 2
22	Crystal structure	1 = aragonitic, 2 = calcitic
23	Albumen	0 = absent, 1 = present
24	Organic core at base of shell unit	0 = absent, 1 = present, 2 = Tuatara type
25	Egg shell pore canals	0 = absent, 1 = present
26	Isolated yolk mass	0 = absent, 1 = present
27	Opaque band of CAM	0 = absent, 1 = present
28	Yolk absorption	1 = endoderm, 2 = cellularized yolk (spaghetti strands), 3 vascularized folds of the extraembryonic endoderm
29	Biomineralized egg shell layers	0 = absent, 1 = 1, 2 = 2 (Tuatara type), 3 = crocodiloid, 4 = multiple layers (avian type)
30	Haematopoietic tissue around blood vessels	0 = absent, 1 = present
31	Nucleus of Pander	0 = absent, 1 = present
32	Air cell	0 = absent, 1 = present
33	Egg asymmetry	0 = absent, 1 = present
34	Capillaries of CAM in shell membrane	0 = absent, 1 = present
35	Chalazae	0 = absent, 1 = present
36	Yolk in multiple organized layers	0 = absent, 1 = present
37	Organic cuticle external to egg shell	0 = absent, 1 = present
38	Eggshell pigmentation	0 = absent, 1 = present
39	Egg turning	0 = absent, 1 = present
40	Reproduction	0 = in water, 1 = on land

[a]Blackburn (2005), Blackburn, 2015a); Morrison et al. (2017).

[b]probably already present in invertebrate chordates (Nelsen, 1953).

[c]vitelline membrane reduced in Euplacentalia.

[d]Long and Ballard (2001) describe the eggs of *Lepisosteus* as: "A second layer of jelly surrounds the chorion. This jelly layer is of variable thickness, up to 0.3 mm, and it provides the sticky character of the eggs." We assume that this sticky jelly layer is an independent evolutionary acquisition and not homologous to the jelly coat of Dipnoi and Amphibia.

[e]*Neoceratodus* has a triple jelly coat (Kemp, 1987), *Lepidosiren paradoxa* has no jelly (Kemp, 1982; Kerr, 1900).

[f]Miyashita and Coates (2015).

[g]Kemp (1987).

[h]Harder (1975).

[i]Dingerkus et al. (1978). The living coelacanth *Latimeria chalumnae* does not have a cloaca.

[j]all three genera of Dipnoi possess a simple cloaca (plesiomorphic condition). Wake (1986).

[k]Wake (1977a).

[l]Sanger et al. (2015); Brennan (2016).

[m]paired in Squamata, but morphologically derived from the midline rudiment of a copulatory organ. Therefore coded like all other Amniota. Our coding does not account for within- amniota diversification (see text for a discussion of parallel evolution of copulatory organs).

[n]prominent in paleognathous birds, ducks, some passerine birds, but reduced in most other birds. King (1981).

[o]Packard (1966), Campbell et al. (1987).

[p]white yolk is always associated with megalecithal eggs. It is probably rather related to the duration of egg deposition as to phylogenetic relationship Riddle, 1911.

[q]Sarasin (1883), Riddle (1911), and Boyd (1940) are the only reference we have been able to find for a latebra in squamates. Cuellar (1971) sought a latebra in *Cnemidophorus* without success, and other reports fail to mention one.

[r]Freyer et al. (2003); Freyer and Renfree (2009).

[s]Freyer et al. (2003); Freyer and Renfree (2009).

[t]Blackburn, Lestz, Barnes, and Powers (2019), Blackburn, Lestz, Barnes, Appiah, and Bonneau (2019); Blackburn (2020).

[u]Dean (1899), Schauinsland (1899, 1903))

[v]Elinson and Stewart (2014); Powers and Blackburn (2017); Blackburn et al. (2018); Blackburn et al. (2019a, 2019b); Blackburn et al. (2020); Blackburn (2020).

[w]Voeltzkow (1901), Blackburn et al. (2020).

[x]Starck (2020).

[y]Depending on phylogeny used, either reduced or ancestrally absent.

FIGURE 17 Phylogeny of vertebrates (Ax, 1984; Mickoleit, 2004; Kuratani & Ota, 2008a, 2008b) with characters discussed in the text. Details and alternative phylogenetic hypotheses are discussed in the text. Characters in brackets refer to in-group diversification, that is, are not autapomorphic for the entire clade
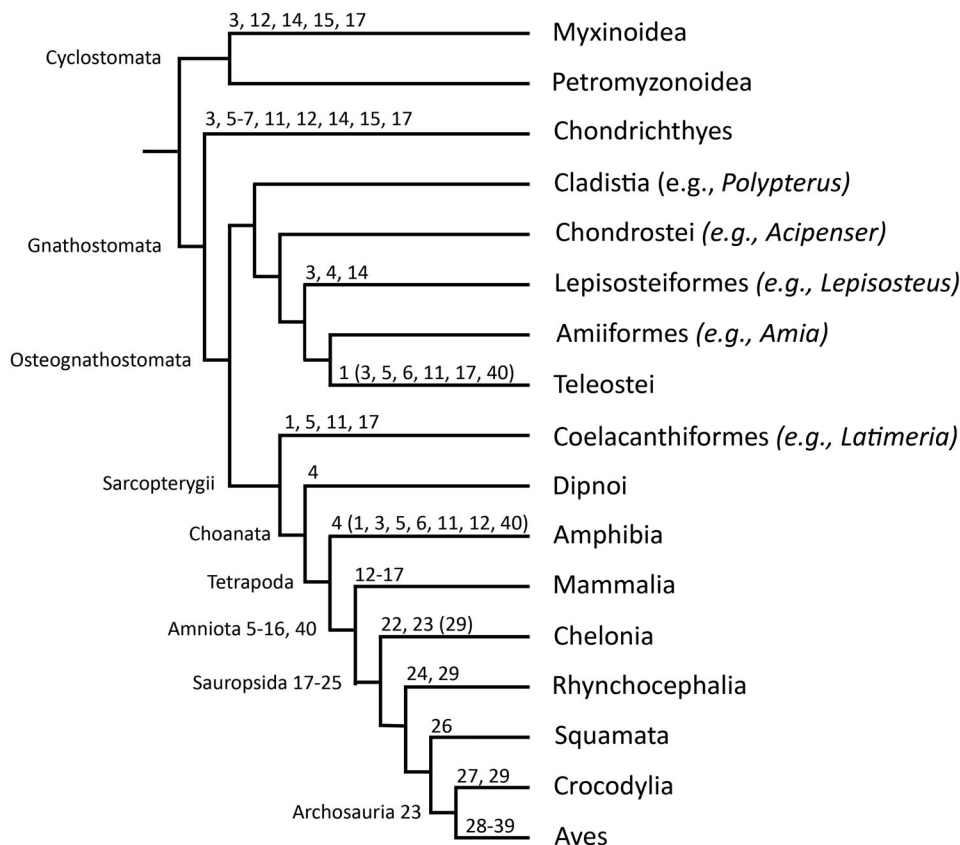
Albumen: Archosaur eggs contain a large volume of albumen as compared with other sauropsids (except turtles). Compared with the crocodilian albumen, the avian albumen is special as it contains the chalazae (suppl. online mat. figure S16), that is, a pair of spirally coiled bands that project from the equatorial region of the vitelline membrane into the albumen. They maintain the yolk in a steady position in the laid egg when the egg is turned. The chalazae contain fibers that appear to be identical with the fibers in the outer layer of the vitelline membrane.

Yolk: The avian yolk is structured in multiple concentric layers of white and yellow yolk laid down around a central core of white yolk, that is, the latebra. The Nucleus of Pander (Pander, 1817a, 1817b; Romanoff & Romanoff, 1949; Starck, 2020) is located below the blastodisc and continues into the neck of the latebra (Figrue 16). While white yolk and latebra have been described for other sauropsids, the degree of structural organization (in particular the layers of yolk) and the Nucleus of Pander distinguish the avian egg from other sauropsids.

Cellular yolk sac: the cellular yolk sac of birds shows a mix of plesiomorphic and autapomorphic features. Development as bi- and tri-laminar omphalopleure is certainly plesiomorphic and results in the cellular yolk sac overgrowing the entire yolk ball, as in other sauropsids (in contrast to squamates that develop an isolated yolk mass). The extraembryonic endoderm of the cellular yolk sac phagocytoses yolk (e.g., Allan-Wojtas, 1994; Lambson, 1970; Mobbs & McMillan, 1979, 1981; Starck, 2018, 2020; Yoshizaki et al., 2004). However, different to all other sauropsids, the endoderm cells always remain superficial to

the yolk ball, and do not cellularize the yolk as described above. Instead, the yolk sac endoderm forms folds that reach into the superficial layers of the yolk mass. These folds carry blood vessels (see detailed description in Starck, 2020, this issue of the Journal of Morphology). The early development of hematopoietic tissue in the yolk sac mesoderm and scattered along the blood vessels (for squamates e.g., Stewart & Florian Jr., 2000; Stewart et al., 2004; Stewart & Thompson, 2017) is certainly a plesiomorphic feature (Claver & Quaglia, 2009), but we miss detailed descriptions for other sauropsids. However, the intensive organization of the hematopoietic tissue in layers around the yolk sac blood vessels is unique for birds and has not been described for any of the other sauropsids. It is therefore considered an autapomorphic character state.

Chorioallantois: The chorioallantois of bird embryos is a typical sauropsid embryonic respiratory organ. However, the diffusion barrier from chorioallantois through shell membranes and biomineralized eggshell is considerably reduced by chorioallantois-capillaries being embedded into the chorionic epithelium. During later development, the capillaries of the chorioallantois deeply protrude into the collagenous fiber network of the inner eggshell membrane further reducing the diffusion barrier (Fancsi & Fehér, 1979; Fitze-Gschwind, 1973; Lusimbo et al., 2000; Maina, 2017; Sethi & Brookes, 1971; Shumko et al., 1988). Such intimate integration of the chorioallantois-capillaries into the chorionic epithelium and even eggshell membranes has not been described for any of the oviparous sauropsids (e.g., Kim & Blackburn, 2015, 2016) and thus is considered a derived character state.
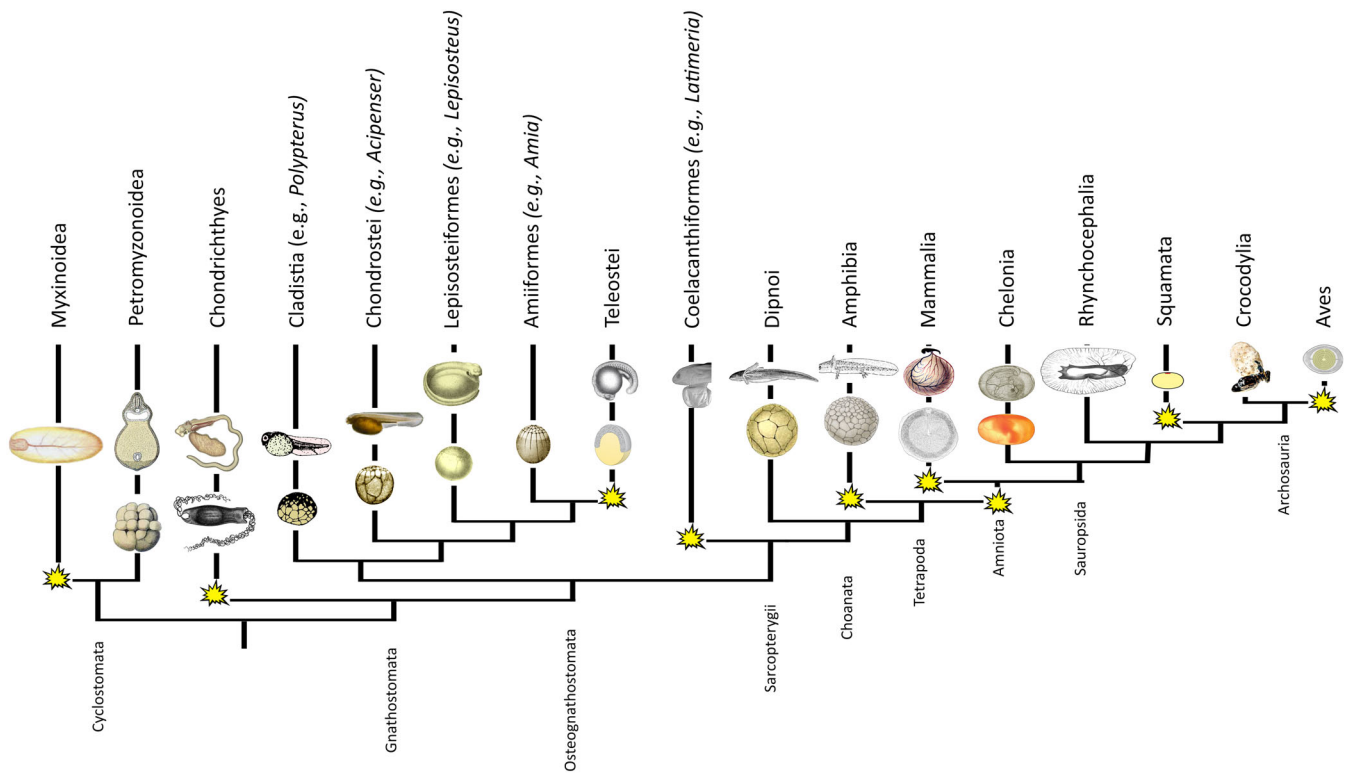
FIGURE 18 Pictorial representation of major transitions of eggs, cleavage pattern and embryos among vertebrates. The star symbol at the base of a clade indicates major morphological changes of egg, cleavage pattern and embryogenesis. Details of the evolutionary changes are given in Figure 17 and Table 1 and discussed in the text. The key message of this figure is that morphological changes, like large yolk, meroblastic cleavage, internal fertilization and egg retention occurred multiple time in phylogenetically independent clades of vertebrates. In some Teleostei and Amphibia plus Amniota they resulted in fully terrestrial reproduction. The amniote egg possibly evolved as an adaptation for egg retention in an aquatic environment that might have been hostile for early egg deposition (intensive egg predation, unfavorable chemical conditions, season of year). The amniote egg may be an exaptation that paved the evolution of terrestrial reproduction. Among amniotes, mammals, squamates and birds are characterized by further clade specific features; therian mammals with respect to viviparity, squamates by the reduction of a solid calcareous egg shell, reduction of albumen and water uptake from the environment, birds by the development of a truly cleidoic egg, being completely independent of the environment (except gas exchange)—at the cost of increased parental care. See text, Figure 17 and Table 1 for a detailed discussion of clade specific features and reconstructions of the ground pattern

3 | PHYLOGENETIC MAPPING AND ANCESTRAL CHARACTER STATE RECONSTRUCTION

3.1 | Vertebrates, ancestral character state reconstruction

The cellular yolk sac (Table 1; character 14) requires a special discussion. Various morphological types of megalecithal eggs and cellular yolk sacs occur in the basal clades of vertebrates (e.g., Myxinoidea: Dean, 1898, 1899; Ota & Kuratani, 2008; Miyashita & Coates, 2015; Elasmobranchii: Musick & Ellis, 2005; Hamlett et al., 2005; teleost fishes: e.g., Kondakova & Efremov, 2014; Kondakova et al., 2017, 2019). Therefore, comparisons for an ancestral character state reconstruction of the egg, cleavage pattern (3), and cellular yolk sac (14) have to reach to the root of the vertebrate phylogeny.

Despite deriving from the same morphological material (i.e., extraembryonic ectoderm, mesoderm and endoderm), the divergent cytoarchitecture of the cellular yolk sacs in these groups, the scattered phylogenetic distribution, and the topology of the vertebrate phylogeny (Figures 17, 18) indicate that these are clade specific independent evolutionary acquisitions of basal vertebrates associated with megalecithal eggs and meroblastic cleavage. Skulan (2000) argued that presence vs. absence of large yolks and of yolk sacs are equivocally parsimonious when plotted on a phylogeny of vertebrates. However, "yolk sac" is a functional term, and as such refers to structures that differ substantially in their cellular and microscopic anatomical organization due to convergent evolution. The ancestral character state of vertebrates (inherited from their non-vertebrate chordate ancestors) is small eggs, holoblastic cleavage, and cellularization of the yolk during gastrulation. This assumption and multiple evolutionary origins of megalecithal eggs with a cellular yolk sac require fewer transitions (five transitions) on a consensus phylogeny than the alternative assumption that a large yolk enclosed by a cellular yolk sac and meroblastic cleavage were basal and reduced in several lineages (six transitions).

3.2 | Gnathostomata, ancestral character state reconstruction

The ancestral character state reconstruction of the egg of Gnathostomata is not without ambiguity, because the ancestral condition for Cyclostomata is only weakly supported, and because Chondrichthyes have megalecithal eggs with a cellular yolk sac. However, supposing that our ancestral character state hypothesis for vertebrates is correct, then small eggs, external fertilization, holoblastic cleavage, and cellularization of the yolk represent an ancestral condition that Cyclostomata (e.g., Petromyzontidae) share as a symplesiomorphy with the stem group of gnathostomes. Among gnathostomes, Polypteriformes, Chondrostei, Amiiformes, Dipnoi and Amphibia maintain this symplesiomorphic condition. Chondrichthyes with their megalecithal eggs and highly derived reproductive mode show a derived condition, including internal fertilization (5) and intromittent organs (6). The unique form of the yolk syncytial layer, epiboly and the organizer center during gastrulation that occur in *Lepisosteus* and Teleostei suggest convergent evolution. Their eggs and yolk sacs differ substantially from the large eggs and yolk sacs found in Myxinoidea and Chondrichthyes, and, of course, amniotes. Admittedly, the interpretation is not without ambiguity and depends on the correct recognition of the ancestral character state for vertebrates. However, we consider the diverging microscopic anatomy of the cellular yolk sac in those basal groups of vertebrates as strong evidence for independent and convergent evolutionary origin.

Other characters listed in the matrix, for example, size of yolk (17), developmental stage at egg deposition (1), cleavage pattern (3), jelly coat (4), and loss of larva (11) appear to be phylogenetically variable and non-informative characters. Copulatory organs (6) and internal fertilization (5) were recently recognized as ancestral gnathostome conditions that occurred already in their extinct stem group. This implies that external fertilization and spawning, which characterize many extant aquatic gnathostomes, derive from internal fertilization (Long et al., 2015). The condition of these character states obviously changed multiple times during vertebrate evolution, often in association with each other, and resulting in superficially convergent morphologies. It is obvious that copulatory organs of Chondrichthyes (claspers), Teleostei (gonopodium), Amphibia (modified cloacal wall) and Amniota (paired genital buds) are independent evolutionary acquisitions. Again, "copulatory organs" refers to a functional term and refers to structures that differ in their cellular and microscopic anatomical organization due to convergent evolution. We have therefore marked four different character states in Table 1. Unfortunately, published data are not detailed enough, or report details of different aspects in different taxa thus impairing comparisons. It would require an independent morphological, microscopic anatomical analysis, and histological analysis of these characters for their fine structural differences to recognize clade specific features and characterize them as independent evolutionary innovation (which is beyond the scope of this review).

3.3 | Osteognathostomata, ancestral character state reconstruction

The ancestral character state reconstruction is again not without ambiguity. Basal Actinopterygii (Cladistia, Chondrostei) have external fertilization, small eggs, and holoblastic cleavage. On the other branch, that is, Sarcopterygii, it is less clear because Coelacanthiformes have derived reproductive features (Table 1, Figure 17); only Dipnoi and Amphibia show the plesiomorphic condition. Again, we find an early diversification of reproductive features, that makes ancestral character state reconstruction weakly supported.

3.4 | Actinopterygii, ancestral character state reconstruction

The ancestral character state of Actinopterygii is probably represented by the small eggs, such as those of Cladistia (*Polypterus)* and Chondrostei (*Acipenser),* holoblastic cleavage and the cellularization of yolk. Meroblastic cleavage and an external, vascularized yolk sac in Lepisosteiformes and teleost fishes may have evolved convergently. The formation of a yolk syncytial layer, lack of endodermal contribution to the yolk sac, and later epiboly by lateral folds of the embryo provide evidence of an independent evolutionary origin. However, Elinson (2009) suggested that change in cleavage occurred already in the stem group of neopterygians (gar, bowfin, and teleosts). In this scenario, meroblastic cleavage evolved in the stem group and so that in *Amia* it was difficult to return to an embryo that divided completely into small cells. From a formal perspective, both hypotheses are equally parsimonious.

3.5 | Sarcopterygii, ancestral character state reconstruction

Latimeria is the only extant representative of the most basal clade of Sarcopterygii. It is viviparous showing numerous viviparity associated morphological modifications of the egg and embryo. Based on our ancestral character state reconstruction of gnathostomes, we are confident that this is a derived condition when compared with Choanata, which represent the plesiomorphic gnathostome condition. Internal fertilization, egg retention, a large yolk sac, and viviparity in *Latimeria* has presumably evolved independently (but see discussion in: Laurin & Reisz, 1997; Laurin & Girondot, 1999; Laurin et al., 2000; Laurin, 2005). Again, a certain degree of ambiguity remains because our ancestral character state reconstruction depends on the correct recognition of the character state in the stem group of Sarcopterygii.

3.6 | Choanata, ancestral character state reconstruction

The two basal branches of Choanata (Dipnoi and Tetrapoda) have small eggs covered with a jelly coat, holoblastic cleavage, and cellularization of

the yolk, which is incorporated into endoderm during gastrulation. After a relatively short embryonic period, a larva hatches and commences feeding. We consider this pattern the ancestral condition they share with basal Actinopterygii, basal gnathostomes and basal vertebrates.

3.7 | Tetrapoda, ancestral character state reconstruction

Fertilization may be external or internal in Amphibia and the laid eggs are relatively small (∼1–2.5 mm). A vitelline membrane and an external jelly coat (sometimes called capsule) cover the yolk; cleavage is holoblastic and a larva hatches from the egg. The sister group, Amniota, has a substantially different reproductive pattern, thus reconstruction of the ancestral character state depends on ingroup pattern and, of course, outgroup comparison (Dipnoi). An enormous diversity of reproductive modes exists among Amphibia (Goin & Goin, 1962; Laurin, 2005, 2010; Laurin et al., 2000; Laurin & Girondot, 1999; Laurin & Reisz, 1997; Martin & Carter, 2013; Sever et al., 2003; Skulan, 2000; Wake, 2015; Wells, 2010; Wilkinson & Nussbaum, 1998). However, careful analyses including basal caecilians show that the ancestral reproductive mode of Amphibia was probably external fertilization (internal in caecilians, but the assumption of external fertilization at the basal node of Amphibia is most parsimonious) of small eggs, holoblastic cleavage, and hatching of a larva. The pattern observed equals that found in Polypteriformes, Chondrostei, Amiiformes and many Teleostei. Thus, we assume that these characters represent the ancestral condition for Tetrapoda. Numerous diverging modes of development, including viviparity and terrestrial reproduction evolved within Amphibia and, of course, within the Amniota.

What results from this comparison is that basal branches of vertebrates, gnathostomes, and tetrapods show a remarkable evolutionary diversification of reproductive modes, egg morphologies, and early embryonic development. Small eggs with holoblastic cleavage from which an early larva hatches represent the vertebrate ground pattern that occurs as plesiomorphic condition in almost all groups. However, in virtually every major clade of vertebrates internal fertilization evolved in certain taxa, that produce large megalecithal eggs with cellular yolk sacs, that delayed egg laying, became independent from water (terrestrial reproduction), or evolved various forms of viviparity. Much of the ancestral character state reconstruction depends not only on the cladogram used, but also on cytological details, and one needs to be aware that functional descriptors (e.g., intromittent organ, large yolk, cellular yolk sac, and eggshell) are often insufficient to grasp the true evolutionary diversity. It requires fine morphological analyses to detect possible independent parallel evolution resulting in highly convergent character complexes.

3.8 | Amniota, ancestral character state reconstruction

Amniota is characterized by a set of well corroborated (some since 150 years ago) reproductive characters, that is, internal fertilization

(5), copulatory organs (6), loss of a larval stage (11), delayed oviposition (1), amnion capable of myogenic contractions (16), chorion (9), allantois (10), egg shell (15; reduced in Marsupialia and Eutheria and in viviparous Squamata), uric acid as excretory product (Packard, 1966; Campbell et al., 1987; 7), white yolk (12), meroblastic cleavage (3, reduced in Theria), the latebra (13) and a cellular yolk sac as described above (14; Table 1; Figure 17).

Recent investigations in vertebrate phallus evolution (Sanger et al., 2015: Brennan, 2016) showed that the amniote phallus had a single evolutionary origin, i.e., intromittent organs are developmentally derived from the same morphological substratum. However, lineage-specific modifications of these homologous structures occurred during evolution of amniote clades, resulting in the morphological diversity of copulatory organs observed in extant amniotes (independent parallel evolution of homologous structures = homoiology; Plate, 1922).

Usually, the chorion and allantois are considered as two separate extraembryonic membranes. This is certainly correct from a morphological point of view. However, neither the ectoderm/ mesoderm-derived chorion nor the endoderm/mesoderm derived allantois are functional as individual membranes. Soon after their appearance, and common to all Amniota, they merge to form a transitory extraembryonic exchange organ (and excreta storing organ). In clades of Amniota that evolved various forms of viviparity, the extraembryonic membranes, yolk sac or chorioallantois, are modified into feto-maternal exchange organs, often in association with the maternal uterus wall.

Because the basal dichotomy of Amniota leads to Mammalia on the one branch, and Sauropsida on the other branch, it is formally difficult, if not impossible, to decide for some characters if they are autapomorphic for Sauropsida, or reduced in Mammalia. The same holds for "myogenic contractions of the amnion," which has not been explicitly described for Monotremata, so that an ultimate evaluation of this character is impossible. From a functional point of view, however, we would expect that it is present in monotremes, because moving of the early embryo is important for development and occurs in all other oviparous amniotes.

3.9 | Sauropsida, ancestral character state reconstruction

The amniote ground pattern as described above can be considered a plesiomorphic condition for the stem group of sauropsids, i.e., internal fertilization, megalecithal eggs, meroblastic cleavage, eggshell, and delayed egg deposition as key reproductive features. The amnion provided a protective and, importantly, myogenically contractile compartment for the developing embryo. The chorioallantois functioned as transitory respiratory organ, site of calcium uptake from the eggshell and, its lumen, as a site for uric acid deposition. However, Sauropsida are also characterized by autapomorphic egg characters (Table 1). Most of these characters are related to the formation of a biomineralized eggshell (24, 25, 29), and the absorption of water from the environment/substratum (20). Also, the structure of the cellular

yolk sac (14) and the pattern of yolk absorption (28) by endodermal cells immigrating into the yolk and only later associating with mesoderm derived blood vessels (forming "spaghetti strands") appears to be an ancestral sauropsid feature. In all sauropsids, the eggshell serves as a depot for calcium (19).

Assuming a phylogeny with turtles as the basal branch of sauropsids, a flexible, two-layered collagenous eggshell membrane containing cores of biomineralization in the outer layer represents the most probable ancestral structure. This eggshell is designed to absorb water from the substratum. The rigid eggshell of some turtles and all archosaurs then evolved convergently in both lines. The reduction of one layer of the eggshell membrane, the reduction of the calcitic layers of the eggshell, and the reduction of the albumen would be considered derived features of squamates.

However, if lepidosaurs are sister to a clade Archelosauria (turtles and archosaurs; Crawford et al., 2015), a single-layered collagenous eggshell membrane containing cores of biomineralization in the outer layer would represent the ancestral sauropsid condition. A two layered-eggshell membrane and rigid eggshell would then have evolved only once in the stem group of Archelosauria (with some reversals among turtles).

Independent of the phylogeny used, the sauropsid ground pattern was modified in all extant clades. The calcium carbonate of Chelonia eggs crystallizes as aragonite (22). The tuatara has a unique structure of the biomineralized eggshell, with large calcitic cones embedded in the eggshell membrane. The reproductive pattern in tuatara probably evolved as adaptation to cold and extreme egg retention. Squamates evolved soft-shelled eggs designed for water uptake from the environment, egg retention, and feto-maternal exchange structures, or, in two lineages of geckos, rigid eggshells (Choi et al., 2018; Fernandez et al., 2015). Squamates are also characterized by the lack of albumen (23), the yolk cleft and the isolated yolk mass (26), a feature of the egg that has escaped a functional explanation. Depending on the phylogenetic position of Chelonia, the lack of albumen would be considered plesiomorphic for sauropsids or secondarily lost in squamates or lepidosaurs.

Archosaurs are difficult to characterize by autapomorphic features. A rigid eggshell is problematic because the layered structure of the crocodilian egg (just one layer of large cones) does not compare directly to the more complex structure of the avian egg (with cone layer, palisades layer and external crystalline layer and cuticle). Archosaur eggs obviously lost the ability for active water uptake from the substratum; instead, they contain all water required for embryonic development in a large volume of albumen that surrounds the central yolk ball. Depending on the phylogeny used, these characters might also be considered a symplesiomorphy that archosaurs share with (some) turtles (it would require that the rigid egg shell, complex structure of the eggshell, and the large volume of albumen are lost / reverted in some taxa of turtles). It is possible that the avian type eggshell derives from the crocodyloid type, by adding additional layers and more sophisticated pore canals. Crocodiles are characterized by the unique growth pattern of the chorioallantois (opaque band; 25).

Bird eggs are characterized by a suite of features (28–39) that can be interpreted in the context of egg turning (39; egg asymmetry, 33; Nucleus of Pander 31; chalazae 35), elevated embryonic metabolism, and fast embryonic growth (hematopoietic tissue around blood vessels, 30; capillaries of CAM deep into shell membrane, 34; air cell, 32), and (additional) protective function of the egg shell (organic cuticle layer external to calcite layer, 37). It remains to be noted that among oviparous sauropsids only extant Chelonia and Archosauria have developed cleidoic eggs that are truly independent of environmental water uptake because they contain the water necessary for embryonic development. In contrast, eggs of Lepidosauria (independent of their phylogenetic relationship to other Sauropsida) with their soft shell and lack of albumen, are functionally designed for water-uptake from the environment. Archosaurs, however, represent a clade in which eggs are fully equipped with water and nutrients enclosed by an eggshell permeable only for respiratory gases and water vapor. Among archosaurs, the avian egg is designed to allow high metabolic rate of the embryos, fast embryonic growth and development, and nesting sites largely independent from the environment—but at the costs of intensive parental care.

4 | EVOLUTIONARY HISTORY OF THE AMNIOTE EGG

Phylogenetic analysis, character mapping, and ancestral character state reconstruction are tools that allow us to recognize the evolution of morphological pattern by bringing them into sequence. Sequences of evolutionary events determined by phylogenetic analysis require functional and ecological explanations. Focusing on the evolution of the amniote egg, this last section presents a hypothesis about the evolutionary history of the amniote egg deduced from phylogenetic analysis and based on functional and comparative explanations.

As a note of caution we would like to reiterate that we see certain advantages and limitations in a review like this, examining evolutionary patterns and processes using analytical techniques currently available. (a) The phylogenetic hypothesis used as the basis for character mapping is, of course, crucial for an interpretation of the data collected. Since phylograms are always working hypotheses of the true relationship among taxa (Hennig, 1966) phylograms may change with changing knowledge, and new interpretations may become prevalent. (b) The nature of data are scattered and heterogeneous in detail. It is evident, that in many cases microscopic anatomical details are missing. Details that would be necessary to understand patterns of convergent evolution (e.g., cellular yolk sac in various clades of vertebrates; structure of the albumen, copulatory organs).—Equally, data of many clades are simply missing. (c) Functional information is often missing and many reports are obscured by topographic anatomical relationship, for example, chorion and allantois are always reported as distinct structures, but they are not. They derive from different morphological substratum, but form one functional organ, that is, the chorioallantois. (d) In our review, detailed ecological information (and examples) has not been included. We provide a narrative that, however, may

stimulate interest and research in the evolutionary morphology of vertebrate reproduction. (e) On the positive side, we think that an overview paper like this helps to recognize patterns of evolution and areas of research that need to be addressed in future. (f) By using an explicit phylogenetic hypothesis and taxon sampling, interpretations and conclusions are more robust than macroevolutionary narratives; in particular, they are reproducible and may be adjusted to improved phylogenetic hypotheses and better taxon sampling.

The established paradigm considers the amniote egg as an evolutionary adaptation to terrestrial reproduction, in which the amnion represents a protective aquarium providing a watery environment for the developing embryo, the yolk sac provides nutrients, the chorioallantois is an exchange organ with the environment (and nitrogen waste storage organ), and the eggshell provides a protective layer that prevents mechanical damage and limits material exchange with the environment (Carroll, 1970, 1991; Luckett, 1977; Packard & Seymour, 1997; Romer, 1957; Szarski, 1968). This scenario is a typical evolutionary narrative from the adaptationist program (Gould & Lewontin, 1979) in which each of the morphological features makes perfect sense as an adaptation to terrestrial reproduction. Without doubt, these ideas are valuable, but the paradigm that has developed from these ideas might be tested by looking at the evolution of the amniote egg in a phylogenetic and comparative framework.

Common features of the reproductive biology of all amniotes are copulatory organs (reduced in tuatara and most birds), internal fertilization, and deposition of eggs containing an embryo that has reached at least the primitive streak or early somite stage. Since intra-oviductal development is not possible without internal fertilization, we consider these features to be functionally connected. A comparative view shows that these features have evolved convergently in various clades of aquatic vertebrates (e.g., Chondrichthyes, *Latimeria*, Teleostei), possibly in response to selective factors such as egg predation or environmental conditions detrimental to the development of (laid) eggs. A copulatory organ and internal fertilization have been described from the stem group of gnathostomes, and thus possibly represents an ancestral gnathostome character (Long et al., 2015). However, the intromittent organs of ancestral vertebrates, Chondrichthyes, Actinopterygii, Gymnophiona, and amniotes are not homologous as evidenced by their highly divergent morphologies. These diverse reproductive structures document that internal fertilization evolved repeatedly and independently in different clades of gnathostomes (Trinajstic et al., 2019). Equally, a large yolk as an energy depot for development, and a cellular yolk sac as an extraembryonic nutrient absorptive organ evolved repeatedly among vertebrates, always in association with delayed egg deposition, intrauterine development, or egg guarding, and often viviparity. All these characters occur in various lines of aquatic anamniotes and none relates primarily to terrestrial reproduction.

The amnion and chorioallantois are exclusive for Amniota. Certainly, the amnion fluid provides a watery environment for the embryo. However, an additional functionally important feature of the amnion membrane is its myogenic contractility that moves the (early) embryo, provides physical separation from the large mass of yolk, and prevents adhering of the growing embryo to extraembryonic

materials. If the amnion evolved as a structure that separates early embryos from the yolk and prevents them from adhering to the eggshell membranes, many of the structures that characterize Amniota (delayed deposition of eggs, large yolk mass, cellular yolk sac, and the amnion) may have evolved in an aquatic environment in association with delayed egg laying. Thus, it is possible, that the amniote egg primarily evolved as a feature facilitating egg retention (probably in response to egg predation, conditions unfavorable for developing eggs, or to ensure that hatching occurs during the favorable season).

The combination of features may have paved the evolutionary pathway for terrestrial reproduction, but rather as an exaptation than an adaptation (Gould & Vrba, 1982). Considering the many independent evolutionary origins of terrestrial reproduction among vertebrates (e.g., discussions in: Laurin & Reisz, 1997; Laurin & Girondot, 1999; Laurin, 2005, 2010; Laurin et al., 2000; Skulan, 2000; Wilkinson & Nussbaum, 1998; Martin & Carter, 2013; Vallin & Laurin, 2004), evolution of the amniote egg presents just one "solution" that enabled the conquest of land for reproduction. Copulatory organs, internal fertilization, delayed egg deposition, and reduction of the number of eggs might have been reproductive features that allowed reproduction on land but they may have evolved under a completely different selective regime, as outlined above.

Amnion and chorioallantois are two exclusive amniote characters that occur together with reproduction on land. The sequence of character states as it results from phylogenetic character mapping presented here, does not provide the necessary resolution to reconstruct the evolutionary history of the amniote egg right at that point of interest. However, we would expect behavioral and structural changes of the egg preceding an evolutionary transition from reproduction in water to reproduction on land. In that sense, evolution of the amniotic egg under aquatic conditions for egg retention, may have paved the evolutionary conquest of land for reproduction. This explanation of the phylogenetic pattern is certainly not in conflict with the classical view that the amniotic egg is a perfect adaptation for reproduction on land as suggested by Romer (1957)—it just shifts the occurrence of many characteristics, including the amnion, to an earlier moment into the (dark) history of the stem group of Amniota and acknowledges that different clades of amniotes have experienced various structural and functional modifications of morphology of the egg.

5 | CONCLUSIONS

We revisited amniote egg morphology in a broad phylogenetic framework. The amniote mode of reproduction and morphology of the egg are characterized by a suite of plesiomorphic and autapomorphic features. Many of these features have convergent evolutionary origins among vertebrates. Fully terrestrial reproduction has evolved independently and convergently in numerous clades of anamniotes. Based on our review, the amniote egg possibly represents an evolutionary adaptation for egg retention in an aquatic environment that might have been hostile for early egg deposition (because of either intensive

egg predation, unfavorable chemical conditions, or to adjust hatching to an optimal season). This view is supported by the largely neglected fact that the amnion shows myogenic contractibility and moves the early embryo, thus preventing adhesion to egg structures rather than providing a container that merely carries the aqueous environment to land. Thus, the amniote egg may be an exaptation that paved the evolution of terrestrial reproduction. The avian egg, despite being paradigmatic referenced as the typical amniote egg, is highly derived, and designed for high metabolic rates and fast growth of embryos.

ACKNOWLEDGMENTS

AUTHOR CONTRIBUTIONS

J. Matthias Starck: conceptualization, methodology, writingoriginal draft, preparing a revision and figures, review and editing. Daniel G. Blackburn: review and editing. James R. Stewart review and editing.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1002/jmor.21380.

DATA AVAILABILITY STATEMENT

This paper reviews literature data, no new data are generated for this study. The data matrix that has been created for this study is accessible as Table 1.

ORCID

J. Matthias Starck https://orcid.org/0000-0001-7882-9482
James R. Stewart https://orcid.org/0000-0001-9032-1163
Daniel G. Blackburn https://orcid.org/0000-0002-0446-6102

ENDNOTE

[1] [...] The blood vessels on the surface of the yolk do not only branch, but also send fine extensions deep into the yolk. The beginning of this (process) is shown in figure 36 and Plate XXXV. These extensions enter (the yolk) from all sides, reaching increasingly deeper into the yolk. During this process they gain in size and branch intensively, so that ultimately a system of fine capillaries penetrates the entire yolk, resulting in a felted mass (of yolk and capillaries). [...] translated by JMS.

REFERENCES

Agassiz, A. (1879). The development of *Lepis*osteus"—Part I. *Proceedings of the American Academy of Arts and Sciences*, vol. xiv.

Agassiz, L. (1857). *Contributions to the natural history of The United States of America, first monograph, volume II, part III – Embryology of the turtle.* Little, Brown and Co.

Allan-Wojtas, P. (1994). Ultrastructural characteristics of yolk in the chicken egg. Mechanisms for yolk absorption and its digestion by the yolk sac at different stages of embryonic development. (Thesis), School of Graduate Studies and Research, Department of Anatomy and Neurobiology, University of Ottawa (Canada).

Altig, R., & McDiarmid, R. W. (2007). Morphological diversity and evolution of egg and clutch structure in amphibians. *Herpetological Monographs*, *21*(1), 1–32.

Augustine, L., & Watkins, B. (2015). Age, fertility and reproductive behavior in Cuban crocodiles, *Crocodylus rhombifer*, at the Smithsonian's National Zoological Park. *Zoo Biology*, *34*, 278–284. https://doi.org/10.1002/zoo.21204

Ax, P. (1984). *Das Phylogenetische System. Systematisierung der lebenden Natur aufgrund ihrer Phylogenese*, (1–349). Stuttgart: Gustav Fischer Verlag.

Ax, P. (2003). *Multicellular animals. Order in nature – System made by man* (Vol. III). Springer Verlag 330 pp.

Balfour, F. M. (1876). On the development of elasmobranch fishes: The general features of the elasmobranch embryo at successive stages. *Journal of Anatomy and Physiology*, *10*, 2–411.

Balfour, F. M., & Parker, W. N. (1882). VII. On the structure and development of *Lepisosteus*. *Philosophical Transactions of the Royal Society*, *173*, 359–442.

Ballard, W. W. (1986). Morphogenetic movements and a provisional fate map of development in the holostean fish *Amia calva*. *Journal of Experimental Zoology*, *238*(3), 355–372.

Ballard, W. W., Mellinger, J., & Lechenault, H. (1993). A series of normal stages for development of *Scyliorhinus canicula*, the lesser spotted dogfish (Chondrichthyes: Scyliorhinidae). *Journal of Experimental Zoology*, *267*(3), 318–336.

Balon, E. K. (1991). Probable evolution of the coelacanth's reproductive style: Lecithotrophy and orally feeding embryos in cichlid fishes and in *Latimeria chalumnae*. *Environmental Biology of Fishes*, *32*, 249–265.

Bartsch, P., Gemballa, S., & Piotrowski, T. (1997). The embryonic and larval development of *Polypterus senegalus* Cuvier, 1829: Its staging with reference to external and skeletal features, behaviour and locomotory habits. *Acta Zoologica*, *78*(4), 309–328.

Bellairs, R. (1961). The structure of the yolk of the hen's egg as studied by electron microscopy: I. the yolk of the unincubated egg. *Journal of Cell Biology*, *11*(1), 207–225.

Benahm, W. B. (1899). The development of the tuatara. *Nature*, *60*(1543), 79–80.

Birchard, G. F., & Deeming, D. C. (2009). Avian eggshell thickness: Scaling and maximum body mass in birds. *Journal of Zoology*, *279*(1), 95–101.

Birchard, G. F., & Reiber, C. L. (1993). A comparison of avian and reptilian chorioallantoic vascular density. *Journal of Experimental Biology*, *178*(1), 245–249.

Birchard, G. F., & Reiber, C. L. (1995). Growth, metabolism, and chorioallantoic vascular density of developing snapping turtles (*Chelydra serpentina*): Influence of temperature. *Physiological Zoology*, *68*(5), 799–811.

Blackburn, D. G. (1982). Evolutionary origins of viviparity in the Reptilia. I. Sauria. *Amphibia-Reptilia*, *3*(2), 185–205.

Blackburn, D. G. (1985). Evolutionary origins of viviparity in the Reptilia. II. Serpentes, Amphisbaenia, and Ichthyosauria. *Amphibia-Reptilia*, *6*(3), 259–291.

Blackburn, D. G. (1998). Structure, function, and evolution of the oviducts of squamate reptiles, with special reference to viviparity and placentation. *Journal of Experimental Zoology*, *282*, 560–617.

Blackburn, D. G. (2000). Reptilian viviparity: Past research, future directions, and appropriate models. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *127*(4), 391–409.

Blackburn, D. G. (2005). Amniote perspectives on the evolutionary origins of viviparity and placentation. In M. C. Uribe & H. J. Grier (Eds.), *Viviparous fishes* (pp. 321–340). New Life Publications, Homestead.

Blackburn, D. G. (2015a). Evolution of vertebrate viviparity and specializations for fetal nutrition: A quantitative and qualitative analysis. *Journal of Morphology*, 276(8), 961–990.

Blackburn, D. G. (2015b). Evolution of viviparity in squamate reptiles: Reversibility reconsidered. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 324, 473–486.

Blackburn, D. G. (2020). Functional morphology, diversity, and evolution of yolk processing specializations in embryonic reptiles and birds. *Journal of Morphology*. https://doi.org/10.1002/jmor.21267

Blackburn, D. G., Barnes, M. S., Reimers, C. D., Appiah, F. A., Lestz, L. L., Bonneau, L. J., Hanson, M., Smith-Paredes, D., & Bhullar, B. A. (2020). How do Crocodylian embryos process yolk? Morphological evidence from the American alligator, *Alligator mississippiensis*. *Journal of Morphology*. 282(7). https://doi.org/10.1002/jmor.21252

Blackburn, D. G., & Flemming, A. F. (2009). Morphology, development, and evolution of fetal membranes and placentation in squamate reptiles. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 312(6), 579–589.

Blackburn, D. G., Johnson, A. R., & Petzold, J. L. (2003). Histology of the extraembryonic membranes of an oviparous snake: Towards a reconstruction of basal squamate patterns. *Journal of Experimental Zoology Part A: Comparative Experimental Biology*, 299(1), 48–58.

Blackburn, D. G., Lestz, L., Barnes, M. S., & Powers, K. G. (2019). How do embryonic turtles process yolk? Evidence from the snapping turtle, *Chelydra serpentina* (Chelydridae). *Canadian Journal of Zoology*, 97, 495–501.

Blackburn, D. G., Lestz, L., Barnes, M. S., Powers, K. G., & Langkilde, T. (2018). Morphological features of the yolk processing pattern in the eastern fence lizard, *Sceloporus undulatus* (Phrynosomatidae). *Journal of Morphology*, 279(11), 1629–1639.

Blackburn, D. G., Lestz, L. L., Barnes, M. S., Appiah, F. A., & Bonneau, L. J. (2019). Ultrastructural analysis of the yolk processing pattern in embryonic pond slider turtles (*Trachemys scripta*: Emydidae). *Journal of Experimental Zoology B*, 332, 187–197.

Blackburn, D. G., & Stewart, J. R. (2011). Viviparity and placentation in snakes. In R. D. Aldridge & D. M. Sever (Eds.), *Reproductive biology and phylogeny of snakes* (Vol. 9, pp. 119–181). Taylor and Francis Group.

Blackburn, D. G., & Stewart, J. R. (2021). Morphological research on amniote eggs and embryos: An introduction and historical retrospective. *Journal of Morphology*. 282(7), https://doi.org/10.1002/jmor.21320

Bolker, J. A. (1993a). Gastrulation and mesoderm morphogenesis in the white sturgeon. *Journal of Experimental Zoology*, 266(2), 116–131.

Bolker, J. A. (1993b). The mechanism of gastrulation in the white sturgeon. *Journal of Experimental Zoology*, 266(2), 132–145.

Bordzilovskaya, N. P., Dettlaf, T. A., Duhan, S. T., & Malacinski, G. M. (1989). Developmental-stage series of axolotl embryos. In J. B. Armstrong & G. M. Malacinski (Eds.), *Developmental biology of the axolotl* (pp. 201–219). Oxford University Press.

Boyd, M. M. (1940). The structure of the ovary and the formation of the corpus luteum in *Hoplodactylus maculatus*, gray. *Quarterly Journal of Microscopical Science*, 82, 337–376.

Brauer, A. (1897). Beiträge zur Kenntnis der Entwicklungsgeschichte und der Anatomie der Gymnophionen. *Zoologische Jahrbücher*, 10, 389–472.

Brennan, P. L. R. (2016). Evolution: one penis after all. *Current Biology*, 26, R29–R31. https://doi.org/10.1016/j.cub.2015.11.024

Buchholz, D. R., Singamsetty, S., Karadge, U., Williamson, S., Langer, C. E., & Elinson, R. P. (2007). Nutritional endoderm in a direct developing frog: A potential parallel to the evolution of the amniote egg. *Developmental Dynamics*, 236, 1259–1272.

Bustard, H. R. (1968). The egg-shell of gekkonid lizards: A taxonomic adjunct. *Copeia*, 1968(1), 162–164.

Caldwell, W. H. (1887). XVI. The embryology of Monotremata and Marsupialia.—Part I. *Philosophical Transactions of the Royal Society of London B*, 178, 463–486.

Callebaut, M., Van Nassauw, L., & Harrisson, F. (1997). Comparison between oogenesis and related ovarian structures in a reptile, *Pseudemys scripta elegans* (turtle) and in a bird *Coturnix coturnix japonica* (quail). *Reproduction Nutrition Development, EDP Sciences*, 37(3), 233–252.

Campbell, J. W., Vorhaben, J. E., & Smith, D. D., Jr. (1987). Uricoteley: Its nature and origin during the evolution of tetrapod vertebrates. *Journal of Experimental Zoology*, 243(3), 349–363.

Campos-Casal, F. H., Cortez, F. A., Gomez, E. I., & Chamut, S. N. (2020). Chemical composition and microstructure of recently oviposited eggshells of *Salvator merianae* (Squamata: Teiidae). *Herpetological Conservation and Biology*, 15(1), 25–40.

Carrier, J. C., Pratt, H. L., & Castro, J. I. (2004). In J. C. Carrier & Heithaus (Eds.), *Reproductive biology of elasmobranchs. In: Biology of sharks and their relatives* (pp. 269–286). CRC Press.

Carroll, R. L. (1970). Quantitative aspects of the amphibian–reptilian transition. *Forma et Functio*, 3, 165–178.

Carroll, R. L. (1991). The origin of reptiles. In H. P. Schultze & L. Trueb (Eds.), *Origins of the higher groups of tetrapods: Controversy and consensus* (pp. 331–335). Comstock Publishing Associates.

Carter, A. M. (2020). The role of mammalian foetal membranes in early embryogenesis: Lessons from marsupials. *Journal of Morphology*. https://doi.org/10.1002/jmor.21140

Carter, A. M. (2021). Thomson Flynn and the monotreme egg from oocyte maturation to germ layer formation. *Journal of Morphology*, 282. https://doi.org/10.1002/jmor.21319

Carvalho, L., & Heisenberg, C. P. (2010). The yolk syncytial layer in early zebrafish development. *Trends in Cell Biology*, 20(10), 586–592.

Chang, C. M., Powrie, W. D., & Fennema, O. (1977). Microstructure of egg yolk. *Journal of Food Science*, 42(5), 1193–1200.

Cherr, G. N., & Clark, W. H., Jr. (1982). Fine structure of the envelope and micropyles in the eggs of the white sturgeon, *Acipenser transmontanus* Richardson. *Development, Growth & Differentiation*, 24(4), 341–352.

Chiari, Y., Cahais, V., Galtier, N., & Delsuc, F. (2012). Phylogenomic analyses support the position of turtles as the sister group of birds and crocodiles (Archosauria). *BMC Biology*, 10(1), 65.

Choi, S., Han, S., Kim, N. H., & Lee, Y. N. (2018). A comparative study of eggshells of Gekkota with morphological, chemical compositional and crystallographic approaches and its evolutionary implications. *PLoS One*, 13(6), e0199496.

Claver, J. A., & Quaglia, A. I. (2009). Comparative morphology, development, and function of blood cells in nonmammalian vertebrates. *Journal of Exotic Pet Medicine*, 18(2), 87–97.

Coleman, J. R., & Terepka, A. R. (1972). Fine structural changes associated with the onset of calcium, sodium and water transport by the chick chorioallantoic membrane. *Journal of Membrane Biology*, 7, 111–127.

Collazo, A., Bolker, J. A., & Keller, R. (1994). A phylogenetic perspective on teleost gastrulation. *The American Naturalist*, 144(1), 133–152.

Collazo, A., & Keller, R. (2010). Early development of *Ensatina eschscholtzii*: an amphibian with a large, yolky egg. *EvoDevo*, 1(1), 1–13.

Conrad, R. M., & Warren, D. C. (1939). The alternate white and yellow layers of yolk in hens' ova. *Poultry Science*, 18(3), 220–224.

Cooper, M. S., & Virta, V. C. (2007). Evolution of gastrulation in the ray-finned (actinopterygian) fishes. *Journal of Experimental Zoology (Molecular and Developmental Evolution)*, 308B, 591–608.

Crawford, N. G., Parham, J. F., Sellas, A. B., Faircloth, B. C., Glenn, T. C., Papenfuss, T. J., Henderson, J. B., Hansen, M. H., & Simison, W. B. (2015). A phylogenomic analysis of turtles. *Molecular Phylogenetics and Evolution*, 83, 250–257. https://doi.org/10.1016/j.ympev.2014.10.021

Cree, A., Cockrem, J. F., & Guillette, L. J. (1992). Reproductive cycles of male and female tuatara (*Sphenodon punctatus*) on Stephens Island, New Zealand. *Journal of Zoology*, 226(2), 199–217.

Cree, A., Guillette, L. J., Jr., & Reader, K. (1996). Eggshell formation during prolonged gravidity of the tuatara *Sphenodon punctatus*. *Journal of Morphology*, 230(2), 129–144.

Cuellar, O. (1971). Reproduction and the mechanism of meiotic restitution in the parthenogenetic lizard *Cnemidophorus uniparens*. *Journal of Morphology*, 133, 139–165.

D'Alba, L., Goldenberg, J., Nallapaneni, A., Zhu, C., Parkinson, D. L., Vanthournout, B., & Shawkey, M. (2021). Evolution of eggshell structure in relation to nesting ecology in non-avian reptiles. *Journal of Morphology* (in press). 282(7).

Dean, B. (1896). Memoirs: The early development of *Amia*. *Journal of Cell Science*, 2(152), 413–444.

Dean, B. (1898). On the development of the Californian hag-fish, *Bdellostoma stouti*, Lockington. *The Quarterly Journal of Microscopical Science*, 40, 269–279.

Dean, B. (1899). On the embryology of *Bdellostoma stouti*. A genera account of myxinoid development from the egg and segmentation to hatching. In *Festschrift zum 70ten Geburtstag Carl von Kupffer* (pp. 220–276). Gustav Fischer.

Dean, B. (1903). An outline of the development of a chimaeroid. *The Biological Bulletin*, 4(5), 270–286.

Dean, B. (1906). *Chimaeroid fishes and their development (no. 32)* (pp. 1–194). Carnegie Institution of Washington.

Deeming, D. C. (2004). In D. C. Deeming (Ed.), *Reptilian incubation: environment, evolution and behaviour*. Nottingham University Press Xiii-349 pp.

Deeming, D. C., & Ruta, M. (2014). Egg shape changes at the theropod–bird transition, and a morphometric study of amniote eggs. *Royal Society Open Science*, 1(3), 140311.

del Pino, E. M., & Elinson, R. P. (1983). A novel development pattern for frogs: Gastrulation produces an embryonic disk. *Nature*, 306(5943), 589–591.

del Pino, E. M., & Escobar, B. (1981). Embryonic stages of *Gastrotheca riobambae* (fowler) during maternal incubation and comparison of development with that of other egg-brooding hylid frogs. *Journal of Morphology*, 167(3), 277–295.

Dendy, A. (1898). Summary of the principal results obtained in a study of the development of the tuatara (*Sphenodon punctatum*). *Proceedings of the Royal Society of London*, 63, 440–443.

Dendy, A. (1899). Memoirs: Outlines of the development of the tuatara, *Sphenodon (Hatteria) punctatus*. *Journal of Cell Science*, 2(165), 1–87.

Desnitskiy, A. G. (2014). On the classification of the cleavage patterns in amphibian embryos. *Russian Journal of Developmental Biology*, 45(1), 1–10.

Desnitskiy, A. G. (2015). On the features of embryonic cleavage in diverse fish species. *Russian Journal of Developmental Biology*, 46(6), 326–332.

Desnitskiy, A. G., & Litvinchuk, S. N. (2015). Comparative and phylogenetic perspectives of the cleavage process in tailed amphibians. *Zygote*, 23 (5), 722–731.

Didier, D. A. (2004). *Phylogeny and classification of extant Holocephali. In: Biology of sharks and their relatives (Carrier, Musick & Heithaus, eds)* (pp. 115–138). CRC Press.

Didier, D. A., LeClair, E. E., & Vanbuskirk, D. R. (1998). Embryonic staging and external features of development of the chimaeroid fish, *Callorhinchus milii* (Holocephali, Callorhinchidae). *Journal of Morphology*, 236(1), 25–47.

Dingerkus, G., Mok, H., & Lagios, M. (1978). The living coelacanth *Latimeria chalumnae* does not have a cloaca. *Nature*, 276, 261–262. https://doi.org/10.1038/276261b0

Doflein, F. (1899). Zur Entwicklungsgeschichte von *Bdellostoma stouti* Lock. *Verhandlungen der deutschen Zoologischen Gesellschaft*, 9, 21–30.

Duellman, W. E., & Trueb, L. (1986). *Biology of amphibians*. MacGraw-Hill.

Dünker, N., Wake, M. H., & Olson, W. M. (2000). Embryonic and larval development in the caecilian *Ichthyophis kohtaoensis* (Amphibia, Gymnophiona): A staging table. *Journal of Morphology*, 243(1), 3–34.

Ecay, T. W., Stewart, J. R., & Blackburn, D. G. (2004). Expression of calbindin-D28K by yolk sac and chorioallantoic membranes of the corn snake, *Elaphe guttata*. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 302(6), 517–525.

Elinson, R. P. (2009). Nutritional endoderm: A way to breach the holoblastic–meroblastic barrier in tetrapods. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 312(6), 526–532.

Elinson, R. P., & Beckham, Y. (2002). Development in frogs with large eggs and the origin of amniotes. *Zoology*, 105(2), 105–117.

Elinson, R. P., & del Pino, E. M. (1985). Cleavage and gastrulation in the egg-brooding, marsupial frog, *Gastrotheca riobambae*. *Development*, 90 (1), 223–232.

Elinson, R. P., & del Pino, E. M. (2012). Developmental diversity of amphibians. *Wiley Interdisciplinary Reviews: Developmental Biology*, 1(3), 345–369.

Elinson, R. P., & Stewart, J. R. (2014). The corn snake yolk sac becomes a solid tissue filled with blood vessels and yolk-rich endodermal cells. *Biology Letters*, 10, 20130870. http://doi.org/10.1098/rsbl.2013.0870

Elinson, R. P., Stewart, J. R., Bonneau, L. J., & Blackburn, D. G. (2014). Amniote yolk sacs: Diversity in reptiles and a hypothesis on their origin. *International Journal of Developmental Biology*, 58, 889–894. https://doi.org/10.1387/ijdb.140239db

Fancsi, T., & Fehér, G. (1979). Ultrastructural studies of chicken embryo chorioallantoic membrane during incubation. *Anatomia, Histologia, Embryologia*, 8(2), 151–159.

Ferguson, M. W. J. (1982). The structure and composition of the eggshell and embryonic membranes *Alligator mississippiensis*. *Transactions of the Zoological Society of London*, 36, 99–152.

Fernandez, V., Buffetaut, E., Suteethorn, V., Rage, J. C., Tafforeau, P., & Kundrát, M. (2015). Evidence of egg diversity in squamate evolution from cretaceous anguimorph embryos. *PLoS One*, 10(7), e0128610.

Ferner, K., & Mess, A. (2011). Evolution and development of fetal membranes and placentation in amniote vertebrates. *Respiratory Physiology & Neurobiology*, 178, 39–50.

Field, D. J., Gauthier, J. A., King, B. L., Pisani, D., Lyson, T. R., & Peterson, K. J. (2014). Toward consilience in reptile phylogeny: MiRNAs support an archosaur, not lepidosaur, affinity for turtles. *Evolution and Development*, 16, 189–196.

Fitze-Gschwind, V. (1973). Zur Entwicklung der Chorioallantoismembran des Hühnchens. *Advances in Anatomy Embryology and Cell Biology*, 47, 1–51.

Flynn, T. T., & Hill, J. P. (1939). The development of the Monotremata. Part IV. Growth of the ovarian ovum, maturation, fertilization and early cleavage. *Transactions of the Zoological Society of London*, 26, 445–622.

Freeman, W. H., & Bracegirdle, B. (1982). *An atlas of embryology* (3rd ed, Vol. 1–94). London: Heinemann Educational Books.

Freyer, C., & Renfree, M. B. (2009). The mammalian yolk sac placenta. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 312, 545–554.

Freyer, C., Zeller, U., & Renfree, M. B. (2003). The marsupial placenta: A phylogenetic analysis. *Journal of Experimental Zoology Part A: Comparative Experimental Biology*, 299, 59–77.

Fricke, H., & Frahm, J. (1992). Evidence for lecithotrophic viviparity in the living coelacanth. *Naturwissenschaften*, 79, 476–479.

Gabrielli, M. G. (2004). Carbonic anhydrases in chick extra-embryonic structures: A role for CA in bicarbonate reabsorption through the chorioallantoic membrane. *Journal of Enzyme Inhibition and Medicinal Chemistry*, 19(3), 283–286.

Gatenby, J. B. (1922). Memoirs: Some notes on the gametogenesis of *Ornithorhynchus paradoxus*. *Journal of Cell Science*, 2(263), 475–496.

Gatenby, J. B., & Hill, J. P. (1924). Memoirs: On an ovum of *Ornithorhynchus* exhibiting polar bodies and polyspermy. *Journal of Cell Science*, 2(270), 229–238.

Gauthier, J. A., Kluge, A. G., & Rowe, T. (1988). The early evolution of the Amniota. In M. K. Benton (Ed.), *The phylogeny and classification of the tetrapods. Volume 1: Amphibians, reptiles, birds* (pp. 103–155). Claredon Press.

Gegenbaur, C. (1870). *Grundzüge der vergleichenden Anatomie*. Wilhelm Engelmann.

Gibbons, J., Nimmagadda, S., & Geetha-Loganathan, P. (2020). The ultrastructure of *Chrysemys picta* eggshell and shell membrane. *American Journal of Zoology*, *3*(1), 10–16.

Giersberg, H. (1922). Untersuchungen über Physiologie und Histologie des Eileiters der Reptilien und Vögel; nebst einem Beitrag zue Fasergenese. *Zeitschrift für Wissenschaftliche Zoologie*, *70*, 1–97.

Gilchrist, J. D. F. (1919). Note on eggs and embryos of the south African myxinoid, *Bdellostoma (Heptatretus) hexatrema*, Müll. *The Quarterly Journal of Microscopical Science*, *63*, 141–168.

Girling, J. E. (2002). The reptilian oviduct: A review of structure and function and directions for future research. *Journal of Experimental Zoology*, *293*(2), 141–170.

Glaesner, L. (1910). Studien zur Entwicklungsgeschichte von *Petromyzon fluviatilis*. *Zoologische Jahrbücher (Anatomie)*, *29*, 139–190.

Glaesner, L. (1925). Normentafel zur Entwicklungsgeschichte des gemeinen Wassermolchs *(Molge vulgaris)*. In F. Keibel (Ed.), *Normentafeln zur Entwicklungsgeschichte der Wirbeltiere* (Vol. 14, pp. 1–49). Gustav Fischer Verlag, Jena.

Goin, O. B., & Goin, C. J. (1962). Amphibian eggs and the montane environment. *Evolution*, *16*, 364–371.

Gorbman, A. (1997). Hagfish development. *Zoological Science*, *14*(3), 375–390.

Gosner, K. L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, *16*, 183–190.

Gould, S. J., & Lewontin, R. C. (1979). The spandrels of san Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, *205*(1161), 581–598.

Gould, S. J., & Vrba, E. S. (1982). Exaptation-a missing term in the science of form. *Paleobiology*, *8*, 4–15.

Gower, D. J., Giri, V., Dharne, M. S., & Shouche, Y. S. (2008). Frequency of independent origins of viviparity among caecilians (Gymnophiona): Evidence from the first 'live-bearing' Asian amphibian. *Journal of Evolutionary Biology*, *21*, 1220–1226.

Grellet-Tinner, G., Chiappe, L. M., Currie, P. J., Koppelhus, E. B., Shugar, M. A., & Wright, J. L. (2004). Dinosaur eggs and nesting: Implications for understanding the origin of birds. In *Feathered dragons: Studies on the transition from dinosaurs to birds* (pp. 185–214). Indiana University Press.

Haeckel, E. (1866). *Generelle Morphologie der Organismen*. Georg Reimer 462 pp.

Hallmann, K., & Griebeler, E. M. (2015). Eggshell types and their evolutionary correlation with life-history strategies in squamates. *PLoS One*, *10*(9), e0138785. https://doi.org/10.1371/journal.pone.0138785

Hamlett, W. C. (2005). Yolk sac and uterine modifications for gestation in chondrichthyans. In M. C. Uribe & H. J. Grier (Eds.), *Viviparous fishes* (pp. 274–288). New Life Publications.

Hamlett, W. C., Kormanik, G., Storrie, M., Stevens, B., & Walker, T. I. (2005). Chondrichthyan parity, lecithotrophy and matrotrophy. *Reproductive biology and phylogeny of Chondrichthyes: Sharks, Batoids, and Chimaeras*, *3*, 395–434.

Hamlett, W. C., Schwartz, F. J., & DiDio, L. J. A. (1987). Subcellular organization of the yolk syncytial-endoderm complex in the preimplantation yolk sac of the shark, *Rhizoprionodon terraenovae*. *Cell and Tissue Research*, *247*(2), 275–285.

Hamlett, W. C., & Wourms, J. P. (1984). Ultrastructure of the preimplantation shark yolk sac placenta. *Tissue and Cell*, *16*(4), 613–625.

Harder, W. (1975). *Anatomy of fishes. Part I. Schweizerbart'sche Verlagsbuchhandlung* (p. 612). Stuttgart.

Hasegawa, M. (2017). Phylogeny mandalas for illustrating the tree of life. *Molecular Phylogenetics and Evolution*, *117*, 168–178.

Hedges, S. B. (2012). Amniote phylogeny and the position of turtles. *BMC Biology*, *10*, 64. https://doi.org/10.1186/1741-7007-10-64

Heemstra, P. C., & Greenwood, P. H. (1992). New observations on the visceral anatomy of the late term fetuses of the living coelacanth fish and the oophagy controversy. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *249*, 49–55.

Hennig, W. (1966). *Phylogenetic systematics*. University of Illinois Press 263 pp.

Hill, J. P. (1933). The development of the Monotremata. Part 2. The structure of the eggshell. *Transactions of the Zoological Society of London*, *21*, 503–544.

Hill, R. V. (2005). Integration of morphological data sets for phylogenetic analysis of Amniota: The importance of integumentary characters and increased taxonomic sampling. *Systematic Biology*, *54*, 530–547.

Hincke, M. T., Nys, Y., Gautron, J., Mann, K., Rodriguez-Navarro, A. B., & McKee, M. D. (2012). The eggshell: Structure, composition and mineralization. *Frontiers inBioscience*, *17*(1266), 80.

Hincke, M. T., Wellman-Labadie, O., McKee, M. D., Gautron, J., Nys, Y., & Mann, K. (2008). Biosynthesis and structural assembly of eggshell components. In Y. Mine (Ed.), *Egg bioscience and biotechnology* (pp. 97–128). Wiley & Sons.

Hirakow, R., & Kajita, N. (1990). An electron microscopic study of the development of amphioxus, *Branchiostoma belcheri tsingtauense*: Cleavage. *Journal of Morphology*, *203*(3), 331–344.

Hirakow, R., & Kajita, N. (1991). Electron microscopic study of the development of amphioxus, *Branchiostoma belcheri tsingtauense*: The gastrula. *Journal of Morphology*, *207*(1), 37–52.

Hirsch, K. F. (1983). Contemporary and fossil chelonian eggshells. *Copeia*, *1983*, 382–397.

Hughes, D. F., & Blackburn, D. G. (2020). Evolutionary origins of viviparity in Chamaeleonidae. *Journal of Zoological Systematics and Evolutionary Research*, *58*(1), 284–302.

Hughes, R. L. (1984). Structural adaptations of the eggs and the fetal membranes of monotremes and marsupials for respiration and metabolic exchange. In R. S. Seymour (Ed.), *Respiration and metabolism of embryonic vertebrates* (pp. 389–421). Dr. W. Junk Publishers.

Hughes, R. L. (1993). Monotreme development with particular reference to the extraembryonic membranes. *Journal of Experimental Zoology*, *266*, 480–494.

Hughes, R. L., Calaby, J. H., & Tyndale-Biscoe, C. H. (1977). Egg membranes and ovarian function during pregnancy in monotremes and marsupials. In J. H. Calaby & C. H. Tyndale-Biscoe (Eds.), *Reproduction and evolution* (pp. 281–291). Canberra: Australian Academy of Science.

Hughes, R. L., & Hall, L. S. (1998). Early development and embryology of the platypus. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *353*(1372), 1101–1114.

Iungman, J., Piña, C. I., & Siroski, P. (2008). Embryological development of *Caiman latirostris* (Crocodylia: Alligatoridae). *Genesis*, *46*(8), 401–417.

Iwabe, N., Hara, Y., Kumazawa, Y., Shibamoto, K., Saito, Y., Miyata, T., & Katoh, K. (2005). Sister group relationship of turtles to the bird crocodilian clade revealed by nuclear DNA–coded proteins. *Molecular Biology and Evolution*, *22*, 810–813.

Jee, J., Mohapatra, B. K., Dutta, S. K., & Sahoo, G. (2016). Sources of calcium for the agamid lizard *Psammophilus blanfordanus* during embryonic development. *Acta Herpetologica*, *11*(2), 171–178.

Jollie, W. P., & Jollie, L. G. (1967). Electron microscopic observations on the yolk sac of the spiny dogfish, *Squalus acanthias*. *Journal of Ultrastructure Research*, *18*, 102–126.

Kemp, A. (1982). The embryological development of the Queensland lungfish, *Neoceratodus forsteri*, (Krefft). *Memoirs of the Queensland Museum*, *20*, 553–397.

Kemp, A. (1987). The biology of the Australian lungfish, *Neoceratodus forsteri* (Kreft 1870). *Journal of Morphology supplement*, *1*, 181–198.

Kemp, A. (1997). Pathology in eggs, embryos, and hatchlings of the Australian lungfish, *Neoceratodus forsteri* (Osteichthyes: Dipnoi). *Copeia*, *1994*, 935–943.

Kemp, A. (2011). Comparison of embryological development in the threatened Australian lungfish *Neoceratodus forsteri* from two sites in a Queensland river system. *Endangered Species Research*, *15*, 87–101.

Kerr, J. G. (1900). The external features in the development of *Lepidosiren paradoxa*, Fitz. *Philosophical Transactions, B*, 192, 299–330.

Kerr, J. G. (1907). The development of *Polypterus senegalus* Cuv. In J. G. Kerr (Ed.), *The works of John Samuel Budgett* (pp. 195–284). Cambridge University Press.

Kim, Y. K., & Blackburn, D. G. (2015). Ultrastructure of the fetal membranes of the oviparous kingsnake, *Lampropeltis getula* (Colubridae) as revealed by scanning electron microscopy. *Journal of Morphology*, 276 (12), 1467–1481.

Kim, Y. K., & Blackburn, D. G. (2016). Fetal membrane ultrastructure and development in the oviparous Milksnake *Lampropeltis triangulum* (Colubridae) with reference to function and evolution in snakes. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 326(5), 290–302.

King, A. S. (1981). In A. S. King & J. McLelland (Eds.), *Phallus. In: Form and function in birds* (Vol. 2, pp. 107–147). Academic Press.

Knupp, C., Chew, M., & Squire, J. (1998). Collagen packing in the dogfish egg case wall. *Journal of Structural Biology*, 122(1–2), 101–110.

Kohring, R. R. (1995). Reflections on the origin of the amniote egg in the light of reproductive strategies and shell structure. *Historical Biology*, 10, 259–275.

Kondakova, E. A., Efremov, V. I., & Bogdanova, V. A. (2017). Structure of the yolk syncytial layer in the larvae of whitefishes: A histological study. *Russian Journal of Developmental Biology*, 48(3), 176–184.

Kondakova, E. A., Efremov, V. I., & Kozin, V. V. (2019). Common and specific features of organization of the yolk syncytial layer of Teleostei as exemplified in *Gasterosteus aculeatus* L. *Biology Bulletin*, 46(1), 26–32.

Kondakova, E. A., Efremov, V. I., & Nazarov, V. A. (2016). Structure of the yolk syncytial layer in Teleostei and analogous structures in animals of the meroblastic type of development. *Biology Bulletin*, 43(3), 208–215.

Kondakova, E. A. A., & Efremov, V. I. I. (2014). Morphofunctional transformations of the yolk syncytial layer during zebrafish development. *Journal of Morphology*, 275(2), 206–216.

Kratochvíl, L., & Frynta, D. (2006). Egg shape and size allometry in geckos (Squamata: Gekkota), lizards with contrasting eggshell structure: Why lay spherical eggs? *Journal of Zoological Systematics and Evolutionary Research*, 44(3), 217–222.

Kudo, T. (1938). In F. Keibel (Ed.), *Normentafeln zur Entwicklungsgeschichte des Japanischen Riesensalamanders (Megalobatrachus japonicus Temmink). Normentafeln zur Entwicklungsgeschichte der Wirbeltiere, Vol 16* (pp. 1–49). Verlag Gustav Fischer.

Kupfer, A., Kramer, A., Himstedt, W., & Greven, H. (2006). Copulation and egg retention in an oviparous caecilian (Amphibia: Gymnophiona). *Zoologischer Anzeiger*, 244, 223–228.

Kupfer, A., Maxwell, E., Reinhard, S., & Kuehnel, S. (2016). The evolution of parental investment in caecilian amphibians: A comparative approach. *Biological Journal of the Linnean Society*, 119(1), 4–14.

Kupffer, C. (1890). Entwicklung von *Petromyzon planeri*. *Archiv für Mikroskopische Anatomie*, 35, 469–558.

Kuraku, S., Hoshiyama, D., Katoh, K., Suga, H., & Miyata, T. (1999). Monophyly of lampreys and hagfishes supported by nuclear DNA–coded genes. *Journal of Molecular Evolution*, 49(6), 729–735.

Kuratani, S., & Ota, K. G. (2008a). Primitive versus derived traits in the developmental program of the vertebrate head: Views from cyclostome developmental studies. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 310(4), 294–314.

Kuratani, S., & Ota, K. G. (2008b). Hagfish (Cyclostomata, vertebrata): Searching for the ancestral developmental plan of vertebrates. *BioEssays*, 30(2), 167–172.

Kusuda, S., Yasukawa, Y., Shibata, H., Saito, T., Doi, O., Ohya, Y., & Yoshizaki, N. (2013). Diversity in the matrix structure of eggshells in the Testudines (Reptilia). *Zoological Science*, 30(5), 366–374.

Lambson, R. O. (1970). An electron microscopic study of the entodermal cells of the yolk sac of the chick during incubation and after hatching. *American Journal of Anatomy*, 129, 1–20.

Laurin, M. (2005). Embryo retention, character optimization, and the origin of the extra-embryonic membranes of the amniotic egg. *Journal of Natural History*, 39(34), 3151–3161.

Laurin, M. (2010). *How vertebrates left the water*. Univ of California Press.

Laurin, M., & Girondot, M. (1999). Embryo retention in sarcopterygians, and the origin of the extra-embryonic membranes of the amniotic egg. In *Annales des sciences naturelles-zoologie et biologie animale* (Vol. 20, pp. 99–104). Elsevier Masson.

Laurin, M., & Reisz, R. R. (1995). A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnaean Society*, 113, 165–223.

Laurin, M., & Reisz, R. R. (1997). A new perspective on tetrapod phylogeny. chap. 2. In S. Sumida & K. L. M. Martin (Eds.), *Amniote origins. Completing the transition to land* (pp. 9–59). Academic Press.

Laurin, M., Reisz, R. R., & Girondot, M. (2000). Caecilian viviparity and amniote origins: A reply to Wilkinson and Nussbaum. *Journal of Natural History*, 34(2), 311–315.

Lawniczak, C. J., & Teece, M. A. (2005). Spatial mobilization of calcium and magnesium from the eggshell of the snapping turtle, *Chelydra serpentina*. *Journal of Herpetology*, 39(4), 659–664.

Lee, M. S. (1997). Pareiasaur phylogeny and the origin of turtles. *Zoological Journal of the Linnaean Society*, 120, 197–280.

Lillywhite, H. B., & Ackermann, R. A. (1984). Hydrostatic pressure, shell compliance and permeability to water vapor in flexible-shelled eggs of the colubrid snake *Elaphe obsoleta*. In R. S. Seymour (Ed.), *Respiration and metabolism of embryonic vertebrates* (pp. 121–135). Dr. W. Junk Publishers.

Long, J. A., Mark-Kurik, E., Johanson, Z., Lee, M. S., Young, G. C., Min, Z., Ahlberg, P. E., Newman, M., Jones, R., den Blaauwen, J., Choo, B., & Trinajstic, K. (2015). Copulation in antiarch placoderms and the origin of gnathostome internal fertilization. *Nature*, 517 (7533), 196–199.

Long, W. L., & Ballard, W. W. (2001). Normal embryonic stages of the longnose gar, *Lepisosteus osseus*. *BMC Developmental Biology*, 1(1), 6.

Luckett, W. P. (1977). Ontogeny of amniote fetal membranes and their application to phylogeny. In M. K. Hecht, P. C. Goody, & B. M. Hecht (Eds.), *Major patterns in vertebrate evolution* (pp. 439–516). Springer.

Lund, R. (1980). Viviparity and intrauterine feeding in a new holocephalan fish from the lower carboniferous of Montana. *Science*, 209(4457), 697–699.

Luong, T. T., Boutillon, M. M., Garrone, R., & Knight, D. P. (1998). Characterization of selachian egg case collagen. *Biochemical and Biophysical Research Communications*, 250(3), 657–663.

Lusimbo, W. S., Leighton, F. A., & Wobeser, G. A. (2000). Histology and ultrastructure of the chorioallantoic membrane of the mallard duck (*Anas platyrhynchos*). *Anatomical Record*, 259(1), 25–34.

Maina, J. N. (2017). Structure and function of the shell and the chorioallantoic membrane of the avian egg: Embryonic respiration. In J. N. Maina (Ed.), *The biology of the avian respiratory system* (pp. 219–247). Cham: Springer. https://doi.org/10.1007/978-3-319-44153-5_9

Martin, K. L., & Carter, A. L. (2013). Brave new propagules: Terrestrial embryos in anamniotic eggs. *Integrative and Comparative Biology*, 53, 233–247. https://doi.org/10.1093/icb/ict018

Marzola, M., Russo, J., & Mateus, O. (2015). Identification and comparison of modern and fossil crocodilian eggs and eggshell structures. *Historical Biology*, 27(1), 115–133. https://doi.org/10.1080/08912963.2013.871009

Menkhorst, E., Nation, A., Cui, S., & Selwood, L. (2009). Evolution of the shell coat and yolk in amniotes: A marsupial perspective. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 312(6), 625–638.

Mickoleit, G. (2004). *Phylogenetische Systematik der Wirbeltiere*. Verlag Dr. Friedrich Pfeil 671 pp.

Mikhailov, K. (1992). The microstructure of avian and dinosaurian eggshell: Phylogenetic implications. In K. E. Campbell, Jr. (Ed.), *Papers in Avian Paleontology Honoring Pierce Brodkorb. Contributions in Science* (pp. 361–373). Natural History Museum of Los Angeles County.

Mikhailov, K. (1997). Fossil and recent eggshell in amniotic vertebrates: Fine structure, comparative morphology and classification. *Special Papers in Palaeontology*, 56, 1–80.

Mikhailov, K. E. (1991). Classification of fossil eggshells of amniotic vertebrates. *Acta Palaeontologica Polonica*, 36(2), 193–238.

Mitsukuri, K. (1891). On the foetal membranes of Chelonia. *Journal of the College of Science, Imperial University, Japan*, 4, 1–53.

Miyashita, T., & Coates, M. I. (2015). Hagfish embryology. In S. L. Edwards & G. G. Goss (Eds.), *Hagfish biology* (pp. 95–128). CRC Press.

Miyashita, T., Coates, M. I., Farrar, R., Larson, P., Manning, P. L., Wogelius, R. A., Edwards, N. P., Anné, J., Bergmann, U., Palmer, A. R., & Currie, P. J. (2019). Hagfish from the cretaceous Tethys Sea and a reconciliation of the morphological–molecular conflict in early vertebrate phylogeny. *Proceedings of the National Academy of Sciences*, 116(6), 2146–2151.

Mobbs, I. G., & McMillan, D. B. (1979). Structure of the endodermal epithelium of the chick yolk sac during early stages of development. *American Journal of Anatomy*, 155, 287–310.

Mobbs, I. G., & McMillan, D. B. (1981). Transport across endodermal cells of the chick yolk sac during early stages of development. *American Journal of Anatomy*, 160, 285–308.

Morisawa, S. (1999). Fine structure of micropylar region during late oogenesis in eggs of the hagfish *Eptatretus burgeri* (Cyclostomata). *Development, Growth & Differentiation*, 41(5), 611–618.

Morrison, K. R., Ngo, V., Cardullo, R. A., & Reznick, D. N. (2017). How fish eggs are preadapted for the evolution of matrotrophy. *Proceedings of the Royal Society B: Biological Sciences*, 284(1867), 20171342.

Mossmann, H. W. (1987). *Vertebrate fetal membranes. Comparative ontogeny and morphology; evolution; phylogenetic significance; basic functions; research opportunities*. McMillan 383 pp.

Musick, J. A., & Ellis, J. K. (2005). Reproductive evolution of chondrichthyans. chap. 3. In W. C. Hamlett (Ed.), *Reproductive biology and phylogeny of chondrichthyes, sharks, batoids and chimaeras* (pp. 45–71). Enfield (NH), USA: Science Publishers, Inc.

Nechaeva, M. V. (2009). Rhythmical contractile activity of amnion in embryogenesis of reptiles and birds. *Journal of Evolutionary Biochemistry and Physiology*, 45(6), 717–723.

Nelsen, O. E. (1953). *Comparative embryology of the vertebrates*. Blakiston Co.

Niermann-Kerkenberg, E., & Hofmann, D. K. (1989). Fertilization and normal development in *Ascidiella aspersa* (Tunicata) studied with Nomarski-optics. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, 43(2), 245–258.

Österström, O., & Lilja, C. (2012). Evolution of avian eggshell structure. *Journal of Morphology*, 273, 241–247.H.

Ota, K. G., & Kuratani, S. (2008). Developmental biology of hagfishes, with a report on newly obtained embryos of the Japanese inshore hagfish, *Eptatretus burgeri*. *Zoological Science*, 25(10), 999–1011.

Packard, G. C. (1966). The influence of ambient temperature and aridity on modes of reproduction and excretion of amniote vertebrates. *The American Naturalist*, 100, 667–682.

Packard, G. C., & Packard, M. J. (1980). Evolution of the cleidoic egg among reptilian antecedents of birds. *American Zoologist*, 20, 351–362.

Packard, G. C., & Packard, M. J. (1988). The physiological ecology of reptilian eggs and embryos. In R. B. Huey (Ed.), *Biology of the reptilia, volume 16, ecology B* (pp. 523–605). Alan R. Liss.

Packard, G. C., Taigen, T. L., Packard, M. J., & Shuman, R. D. (1979). Water-vapor conductance of testudinian and crocodilian eggs (class Reptilia). *Respiration Physiology*, 38(1), 1–10.

Packard, G. C., Tracy, C. R., & Roth, J. J. (1977). The physiological ecology of reptilian eggs and embryos and the evolution of viviparity within the class Reptilia. *Biological Reviews*, 52(1), 71–105.

Packard, M. J. (1980). Ultrastructural morphology of the shell and shell membrane of eggs of common snapping turtles (*Chelydra serpentina*). *Journal of Morphology*, 165(2), 187–204.

Packard, M. J. (1994). Patterns of mobilization and deposition of calcium in embryos of oviparous, amniotic vertebrates. *Israel Journal of Zoology*, 40, 481–492.

Packard, M. J., Burns, L. K., Hirsch, K. F., & Packard, G. C. (1982). Structure of shells of eggs of *Callisaurus draconoides* (Reptilia, Squamata, Iguanidae). *Zoological Journal of the Linnean Society*, 75(4), 297–316.

Packard, M. J., & DeMarco, V. G. (1991). Eggshell structure and formation in eggs of oviparous reptiles. In D. C. Deeming & M. W. J. Ferguson (Eds.), *Egg incubation: its effects on embryonic development in birds and reptiles* (pp. 53–69). Cambridge University Press.

Packard, M. J., Hirsch, K. F., & Iverson, J. B. (1984). Structure of shells from eggs of kinosternid turtles. *Journal of Morphology*, 181(1), 9–20.

Packard, M. J., Hirsch, K. F., & Meyer-Rochow, V. B. (1982). Structure of the shell from eggs of the tuatara, *Sphenodon punctatus*. *Journal of Morphology*, 174(2), 197–205.

Packard, M. J., & Packard, G. C. (1979). Structure of the shell and tertiary membranes of eggs of softshell turtles (*Trionyx spiniferus*). *Journal of Morphology*, 159(1), 131–143.

Packard, M. J., & Packard, G. C. (1984). Comparative aspects of calcium metabolism in embryonic reptiles and birds. In R. S. Seymour (Ed.), *Respiration and metabolism of embryonic vertebrates* (pp. 155–179). Springer.

Packard, M. J., & Packard, G. C. (1989). Mobilization of calcium, phosphorus, and magnesium by embryonic alligators *Alligator mississippiensis*. *American Journal of Physiology*, 257, R1541–R1547.

Packard, M. J., & Packard, G. C. (1991). Sources of calcium, magnesium, and phosphorus for embryonic softshell turtles (*Trionyx spiniferus*). *Journal of Experimental Zoology*, 258, 151–157.

Packard, M. J., & Seymour, R. S. (1997). In S. S. Sumida & K. L. M. Martin (Eds.), *Amniote origins* (pp. 265–290). Academic Press.

Packard, M. J., Short, T. M., Packard, G. C., & Gorell, T. A. (1984). Sources of calcium for embryonic development in eggs of the snapping turtle *Chelydra serpentina*. *Journal of Experimental Zoology*, 230(1), 81–87.

Packard, M. J., Thompson, M. B., Goldie, K. N., & Vos, M. (1988). Aspects of shell formation in eggs of the tuatara, *Sphenodon punctatus*. *Journal of Morphology*, 197(2), 147–157.

Pander, C. (1817a). Historiam metamorphoseos, quam ovum incubatum prioribus quinque diebus subit. (Dissertation inauguralis), facultas medicinae, Wirceburgi 1817.

Pander, C. (1817b). Beiträge zur Entwickelungsgeschichte des Hühnchens in Eye. Heinrich Ludwig Brönner, Frankfurt /M. pp. 1–52.

Park, C., Lee, S. Y., Kim, D. S., & Nam, Y. K. (2013). Embryonic development of Siberian sturgeon *Acipenser baerii* under hatchery conditions: An image guide with embryological descriptions. *Fisheries and Aquatic Sciences*, 16(1), 15–23.

Pasteels, J. (1958). Developpement des Agnathes. In P. P. Grassé (Ed.), *Traité de Zoologie. Anatomie, Systématique, Biologie. Tome XIII, premiere fascicule* (pp. 106–144). Masson et Cie Èditeurs.

Perry, M. M., & Gilbert, A. B. (1985). The structure of yellow yolk in the domestic fowl. *Journal of Ultrastructure Research*, 90(3), 313–322.

Piavis, G. W. (1961). Embryological stages in the sea lamprey and effects of temperature on development. *Fishery Bulletin of the Fish and Wildlife Service*, 61, 111–143.

Piavis, G. W. (1971). Embryology. In M. W. Hardisty & I. C. Potter (Eds.), *The biology of lampreys, vol. 1* (pp. 361–400). Academic Press.

Pike, D. A., Andrews, R. M., & Du, W. G. (2012). Eggshell morphology and gekkotan life-history evolution. *Evolutionary Ecology*, 26(4), 847–861.

Plate, L. (1922). *Allgemeine Zoologie und Abstammungslehre: 1*. Teil.

Powell, M. L., Kavanaugh, S. I., & Sower, S. A. (2005). Current knowledge of hagfish reproduction: Implications for fisheries management. *Integrative and Comparative Biology*, 45(1), 158–165.

Powers, K. G., & Blackburn, D. G. (2017). A novel pattern of yolk processing in developing snake eggs (Colubridae: Lampropeltini) and its functional and evolutionary implications. *Journal of Experimental*

Zoology Part B: Molecular and Developmental Evolution, 328B, 462–475.

Rahn, H., & Paganelli, C. V. (1989). Shell mass, thickness and density of avian eggs derived from the tables of Schönwetter. *Journal für Ornithologie*, 130(1), 59–68.

Rathke, H. (1866). *Untersuchungen über die Entwickelung und den Körperbau der Krokodile* (pp. 1–275). Verlag Friedrich von Vieweg und Sohn.

Reese, A. M. (1908). *Development of the American alligator (A. mississippiensis)* (pp. 1–111). Smithsonian Institution Publication 1791.

Richardson, M. K., Admiraal, J., & Wright, G. M. (2010). Developmental anatomy of lampreys. *Biological Reviews*, 85(1), 1–33.

Richardson, M. K., & Wright, G. M. (2003). Developmental transformations in a normal series of embryos of the sea lamprey *Petromyzon marinus* (Linnaeus). *Journal of Morphology*, 257(3), 348–363.

Ricklefs, R. E., & Starck, J. M. (1998). Embryonic growth and development. In: *Avian growth and development. Evolution within the altricial-precocial spectrum* (Starck, J. M. & Ricklefs R. E., eds.). *Oxford Ornithology Series*, 8, 31–58.

Riddle, O. (1911). On the formation, significance and chemistry of the white and yellow yolk of ova. *Journal of Morphology*, 22(2), 455–491.

Rieppel, O. (2000). Turtles as diapsid reptiles. *Zoologica Scripta*, 29(3), 199–212.

Rieppel, O., & DeBraga, M. (1996). Turtles as diapsid reptiles. *Nature*, 384 (6608), 453–455.

Riley, C. J., Sturrock, J., Mooney, S. J., & Luck, M. R. (2014). Quantification of eggshell microstructure using X-ray micro computed tomography. *British Poultry Science*, 55(3), 311–320. https://doi.org/10.1080/00071668.2014.924093

Romanoff, A. L., & Romanoff, A. J. (1949). *The avian egg*. John Wiley and Sons, Inc.

Romer, A. S. (1957). Origin of the amniote egg. *The Scientific Monthly*, 85 (2), 57–63.

Rugh, R. (1951). *The frog, its reproduction and development*. The Blakiston Company.

Salthe, S. N. (1963). The egg capsules in the Amphibia. *Journal of Morphology*, 113(2), 161–171.

Sanger, T. J., Gredler, M. L., & Cohn, M. J. (2015). Resurrecting embryos of the tuatara, *Sphenodon punctatus*, to resolve vertebrate phallus evolution. *Biology Letters*, 11, 20150694. https://doi.org/10.1098/rsbl.2015.0694

Sarasin, C. F. (1883). In C. Semper (Ed.), *Reifung und Furchung der Reptilieneier. Arbeiten aus dem Zoologisch-Zootomischen Institut in Würzburg* (Vol. 6, pp. 159–216). C. W. Kreidel's Verlag.

Sarasin, P., & Sarasin, F. (1887). *Zur Entwicklungsgeschichte und Anatomie der ceylonesischen Blindwühle Ichthyophis glutinosus*. CW Kreidel.

Scammon, R. E. (1911). In F. Keibel (Ed.), *Normal plates of the development of Squalus acanthias. Normentafeln zur Entwicklungsgeschichte der Wirbeltiere, Heft 12*. Gustav Fischer Verlag 140 pp.

Schauinsland, H. (1899). Beiträge zur Biologie und Entwicklung der *Hatteria* nebst Bemerkungen über die Entwicklung der Sauropsiden: *Anatomischer Anzeiger* XV. Bd. 1899.

Schauinsland, H. (1903). Beiträge zur Entwicklungsgeschichte und Anatomie der Wirbeltiere III. Beiträge zur Kenntnis der Eihäute der Sauropsiden. *Zoologica*, 39, 146–168.

Schwann, T. H. (1847). *Microscopical researches into the accordance in the structure and growth of animals and plants*. Adlard, Printers, Sydenham Society 314 pp.

Semon, R. (1894). Die Embryonalhüllen der Monotremen und Marsupialier. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena*, 5, 19–58.

Sethi, N., & Brookes, M. U. R. R. A. Y. (1971). Ultrastructure of the blood vessels in the chick allantois and chorioallantois. *Journal of Anatomy*, 109, 1–15.

Sever, D. M., Hamlett, W. C., Slabach, R., Stephenson, B., & Verrell, P. A. (2003). Internal fertilization in the Anura with special reference to mating and femal sperm storage in *Ascaphus*. Chap. 7. In B. G. M. Jamieson (Ed.), *Reproductive biology and phylogeny* (Vol. 2, pp. 319–341). Science Publishers.

Seymour, R. S., & Ackerman, R. A. (1980). Adaptations to underground nesting in birds and reptiles. *American Zoologist*, 20(2), 437–447.

Shimizu, S., & Ota, H. (2003). Normal development of *Microhyla ornate*. The first description of the complete embryonic and larval stages for the microhylid frogs (Amphibia: Anura). *Current Herpetology*, 22(2), 73–90.

Shumko, J. Z., Defouw, D. O., & Feinberg, R. N. (1988). Vascular histodifferentiation in the chick chorioallantoic membrane: A morphometric study. *Anatomical Record*, 220, 179–189.

Siegel, D. S., Miralles, A., Chabarria, R. E., & Aldridge, R. D. (2011). Female reproductive anatomy: Cloaca, oviduct, and sperm storage. In D. Sever & R. Aldridge (Eds.), *Reproductive biology and phylogeny of snakes* (pp. 347–409). CRC Press.

Siegel, D. S., Miralles, A., Reubert, J. L., & Sever, D. M. (2015). Female reproductive anatomy: Cloaca, oviduct, and sperm storage. In J. L. Rheubert, D. S. Siegel, & S. E. Trauth (Eds.), *Reproductive biology and phylogeny of lizards and tuatara* (pp. 144–195). CRC Press.

Skulan, J. (2000). Has the importance of the amniote egg been overstated? *Zoological Journal of the Linnean Society*, 130(2), 235–261.

Stach, T., Winter, J., Bouquet, J. M., Chourrout, D., & Schnabel, R. (2008). Embryology of a planktonic tunicate reveals traces of sessility. *Proceedings of the National Academy of Sciences*, 105(20), 7229–7234.

Starck, J. M. (1989). Zeitmuster der Ontogenesen bei nestflüchtenden und-nesthockenden Vögeln. *Courier Forschungsinstitut Senckenberg*, 114, 1–318.

Starck, J. M. (1993). Evolution of avian ontogenies. In *Current Ornithology* (pp. 275–366). Springer.

Starck, J. M. (1999). Functional capacities of extraembryonic organs in bird embryos. In N. J. Adams & R. H. Slotow (Eds.), *Proceedings of the 22nd international ornithological congress* (pp. 2836–2856). BirdLife South Africa.

Starck, J. M. (2018). From fertilization to independence. Chap. 5. In M. L. Morrison, A. D. Rodewald, G. Voelker, M. R. Colón, & J. F. Prather (Eds.), *Ornithology: Foundation, critique, and application* (pp. 97–128). Johns Hopkins University Press.

Starck, J. M. (2020). Morphology of the avian yolk sac. *Journal of Morphology*. https://doi.org/10.1002/jmor.21262

Starck, J. M., & Ricklefs, R. E. (Eds.). (1998). *Avian growth and development: Evolution within the Altricial-Precocial Spectrum*. Oxford University Press 441 pp.

Stewart, J. R. (1985). Placentation in the lizard, *Gerrhonotus coeruleus*, with a comparison to the extraembryonic membranes of the oviparous, *Gerrhonotus multicarinatus* (Sauria: Anguidae). *Journal of Morphology*, 185, 101–114.

Stewart, J. R. (1990). Development of the extraembryonic membranes and histology of the placentae in *Virginia striatula* (Squamta: Serpentes). *Journal of Morphology*, 205, 33–43.

Stewart, J. R. (1993). Yolk sac placentation in reptiles: Structural innovation in a fundamental vertebrate nutritional system. *JJournal of Experimental Zoology*, 266, 431–449.

Stewart, J. R. (1997). Morphology and evolution of the egg of oviparous amniotes. Chap. 9. In S. Sumida & K. L. M. Martin (Eds.), *Amniote origins. Completing the transition to land* (pp. 291–326). Academic Press.

Stewart, J. R. (2013). Fetal nutrition in lecithotrophic squamate reptiles: Toward a comprehensive model for evolution of viviparity and placentation. *Journal of Morphology*, 274(7), 824–843.

Stewart, J. R. (2020). Developmental morphology and evolution of extraembryonic membranes of lizards and snakes (Reptilia, Squamata). *Journal of Morphology*. https://doi.org/10.1002/jmor.21266

Stewart, J. R., & Blackburn, D. G. (2019). A developmental synapomorphy of squamate reptiles. *Evolution & Development*, 21(6), 342–353.

Stewart, J. R., Ecay, T. W., & Blackburn, D. G. (2004). Sources and timing of calcium mobilization during embryonic development of the corn snake, *Pantherophis guttatus*. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, 139, 335–341.

Stewart, J. R., & Florian, J. D., Jr. (2000). Ontogeny of the extraembryonic membranes of the oviparous lizard, *Eumeces fasciatus* (Squamata: Scincidae). *Journal of Morphology*, 244, 81–107.

Stewart, J. R., Russell, K. J., & Thompson, M. B. (2012). Development of yolk sac and chorioallantoic membranes in the Lord Howe Island skink, *Oligosoma lichenigerum*. *Journal of Morphology*, 273(10), 1163–1184.

Stewart, J. R., & Thompson, M. B. (2017). Yolk sac development in lizards (Lacertilia: Scincidae): New perspectives on the egg of amniotes. *Journal of Morphology*, 278(4), 574–591.

Stoddard, M. C., Sheard, C., Akkaynak, D., Yong, E. H., Mahadevan, L., & Tobias, J. A. (2019). Evolution of avian egg shape: Underlying mechanisms and the importance of taxonomic scale. *IBIS*, 161, 922–925.

Stoddard, M. C., Yong, E. H., Akkaynak, D., Sheard, C., Tobias, J. A., & Mahadevan, L. (2017). Avian egg shape: Form, function, and evolution. *Science*, 356, 1249–1254.

Stolfi, A., & Brown, F. D. (2015). Tunicata. In *Evolutionary developmental biology of invertebrates* (Vol. 6, pp. 135–204). Springer.

Svensson, G. S. (1938). Zur Kenntnis der Furchung bei den Gymnophionen. *Acta Zoologica*, 19(1–2), 191–207.

Szarski, H. (1968). The origin of vertebrate foetal membranes. *Evolution*, 22, 211–214.

TeWinkel, L. E. (1943). Observations on later phases of embryonic nutrition in *Squalus acanthias*. *Journal of Morphology*, 73(1), 177–205.

Thompson, M. B. (1987). Water exchange in reptilian eggs. *Physiological Zoology*, 60(1), 1–8.

Trinajstic, K., Boisvert, C., Long, J. A., & Johanson, Z. (2019). Evolution of vertebrate reproduction. Chapter 12. In Z. Johanson, C. Underwood, & M. Richter (Eds.), *Evolution and Development of Fishes* (pp. 207–226). Cambridge University Press.

Turpaev, T. M., & Nechaeva, M. V. (2000). Extraembryonic motor activity during the embryogenesis of higher vertebrates. *Neuroscience and Behavioral Physiology*, 30(1), 9–14.

Tyndale-Biscoe, H., & Renfree, M. (1987). *Reproductive physiology of marsupials*. *Monographs on Marsupial Biology*. Cambridge University press 476 pp.

Vallin, G., & Laurin, M. (2004). Cranial morphology and affinities of *Microbrachis*, and a reappraisal of the phylogeny and lifestyle of the first amphibians. *Journal of Vertebrate Paleontology*, 24(1), 56–72.

Voeltzkow, A. (1901). Beiträge zur Entwicklungsgeschichte der Reptilien. IV. Keimblätter, Dottersack und erste Anlage des Blutes und der Gefäße bei *Crocodilus madagascariensis*. 5 Abbildungen, 7 Tafeln, 231, 339-418.

Wake, M. H. (1972). Evolutionary morphology of the caecilian urogenital system. IV. The cloaca. *Journal of Morphology*, 136(3), 353–365.

Wake, M. H. (1977a). The reproductive biology of caecilians: An evolutionary perspective. In D. H. Taylor & S. I. Guttman (Eds.), *The reproductive biology of amphibians*. Springer. https://doi.org/10.1007/978-1-4757-6781-0_3

Wake, M. H. (1977b). Fetal maintenance and its evolutionary significance in the Amphibia: Gymnophiona. *Journal of Herpetology*, 11(4), 379–386.

Wake, M. H. (1978). The reproductive biology of *Eleutherodactylus jasperi* (Amphibia, Anura, Leptodactylidae), with comments on the evolution of live-bearing systems. *Journal of Herpetology*, 12, 121–133.

Wake, M. H. (1986). Urogenital morphology of dipnoans, with comparisons to other fishes and to amphibians. *Journal of Morphology Supplement*, 1, 199–216.

Wake, M. H. (1992). Evolutionary scenarios, homology and convergence of structural specializations for vertebrate viviparity. *American Zoologist*, 32(2), 256–263.

Wake, M. H. (1993). Evolution of oviductal gestation in amphibians. *Journal of Experimental Zoology*, 266(5), 394–413.

Wake, M. H. (2015). Fetal adaptations for viviparity in amphibians. *Journal of Morphology*, 276(8), 941–960.

Walvig, F. (1963). The gonads and the formation of the sexual cells. In A. Brodal & R. Fänge (Eds.), *The biology of Myxine* (pp. 530–580). Universitetforlaget.

Wang, S., Zhao, L., Liu, L., Yang, D., Khatiwada, J. R., Wang, B., & Jiang, J. (2017). A complete embryonic developmental table of *Microhyla fissipes* (Amphibia, Anura, Microhylidae). *Asian Herpetological Research*, 8, 108–117.

Webb, G., Manolis, S. C., Whitehead, P. J., & Dempsey, K. (1987). The possible relationship between embryo orientation opaque banding and the dehydration of albumen in crocodile eggs. *Copeia*, 1987(1), 252–257.

Wells, K. D. (2010). *The ecology and behavior of amphibians*. University of Chicago Press.

Werneburg, I., & Sánchez-Villagra, M. R. (2009). Timing of organogenesis support basal position of turtles in the amniote tree of life. *BMC Evolutionary Biology*, 9(1), 1–9.

Whitman, C. O., & Eycleshymer, A. C. (1897). The egg of *Amia* and its cleavage. *Journal of Morphology*, 12(2), 309–354.

Wilkinson, M., & Nussbaum, R. A. (1998). Caecilian viviparity and amniote origins. *Journal of Natural History*, 32(9), 1403–1409.

Willoughby, B., Steyn, L., Bam, L., Olivier, A. J., Devey, R., & Maina, J. N. (2016). Micro-focus X-ray tomography study of the microstructure and morphometry of the eggshell of ostriches (*Struthio camelus*). *The Anatomical Record*, 299(8), 1015–1026.

Wink, C. S., Elsey, R. M., & Bouvier, M. (1990). Porosity of eggshells from wild and captive, pen-reared alligators (*Alligator mississippiensis*). *Journal of Morphology*, 203(1), 35–39.

Wourms, J. P. (1977). Reproduction and development in chondrichthyan fishes. *American Zoologist*, 17(2), 379–410.

Wourms, J. P., Atz, J. W., & Stribling, M. D. (1991). Viviparity and the maternal-embryonic relationship in the coelacanth *Latimeria chalumnae*. In J. A. Musick, M. N. Bruton, & E. K. Balon (Eds.), *The biology of Latimeria chalumnae and evolution of coelacanths*. *Developments in environmental biology of fishes* (Vol. 12). Springer.

Yoshizaki, N., Soga, M., Ito, Y., Mao, K. M., Sultana, F., & Yonezawa, S. (2004). Two-step consumption of yolk granules during the development of quail embryos. *Development, Growth & Differentiation*, 46, 229–238.

Zardoya, R., & Meyer, A. (1998). Complete mitochondrial genome suggests diapsid affinities of turtles. *Proceedings of the National Academy of Science*, 95, 14226–14231.