JOURNAL OF MORPHOLOGY 00:00–00 (2015)

Morphological Specializations for Fetal Maintenance in Viviparous Vertebrates: An Introduction and Historical Retrospective

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ABSTRACT In many viviparous vertebrates, pregnant females sustain their developing embryos and provide them with nutrients by means of placentas and a diversity of other types of specializations. With this article, we introduce a virtual (online) issue of the *Journal of Morphology* that presents 12 recent papers on fetal maintenance in viviparous vertebrates. We also outline the history of research in this area and document the central role of morphology in helping to explain the function and evolution of specializations for fetal nutrition. This virtual issue of the *Journal of Morphology* is an outgrowth of a symposium held under auspices of the International Congress of Vertebrate Morphology. The included papers reflect a diversity of taxa, research methods, and biological issues. To celebrate the publication of this virtual issue of the *Journal of Morphology*, the publisher is making freely available to readers a number of other relevant papers published in the journal over the past 128 years. J. Morphol. 000:000–000, 2015. © 2015 Wiley Periodicals, Inc.

KEY WORDS: history of science; viviparity; matrotrophy; fetal nutrition; morphology

INTRODUCTION

In viviparous vertebrates, pregnant females maintain developing embryos in their reproductive tracts from the time of fertilization until birth. To meet the respiratory and nutritional needs of these embryos, vertebrates have evolved a remarkable diversity of specializations, including placentas and other features that accomplish maternal–fetal nutrient transfer. Such specializations have fascinated biologists for centuries, and their structure, function, and evolution constitute active areas of research.

This article is an introduction to a virtual (online) issue of the *Journal of Morphology*, one that presents 12 recent papers on morphological specializations for fetal maintenance in live-bearing vertebrates. The genesis of this virtual issue was a symposium entitled “Fetal Nutritional Specializations in Viviparous Vertebrates” held at the Tenth International Congress of Vertebrate Morphology (ICVM) in Punta del Este, Uruguay in 2010, and organized by Daniel G. Blackburn and James R. Stewart. The symposium participants and other researchers represented in this journal issue are using a variety of research methods to study a diversity of organisms. Their shared goal is to understand the mechanisms by which viviparous females maintain their developing embryos. In association with this commemorative issue of the *Journal of Morphology*, the publishers are making freely available to readers a number of other relevant papers that have appeared in this journal since the 1880s through the present. In this introductory paper, we explore relevant conceptual distinctions, the role of morphology in studies of specializations for fetal sustenance, and the historical background of research in this area. In addition, we summarize the nature and scope of the papers that make up this virtual issue of the journal.

OVERARCHING ISSUES

Conceptual Distinctions

The distinction between animals that lay eggs and those that give birth to their young is a fundamental one that dates in the biological literature to the writings of Aristotle. Although various biological terms have been applied to this distinction, in the contemporary literature “oviparity” and “viviparity” commonly are used to describe “egg-laying reproduction” and “live-bearing reproduction” respectively (e.g., Wourms, 1981; Blackburn, 1992, 2000a; Wake, 2002; Musick and Ellis, 2005). Under this usage, “viviparity” refers to species in which embryos develop in the maternal

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Received 15 February 2015;
Accepted 11 May 2015.

DOI 10.1002/jmor.20410

reproductive tract. (The term "embryo" is used here in the broad sense, to include developing offspring that are conventionally called "larvae" and "fetuses." For a broader use of the term "viviparity," see Wake, in press). For oviparous anurans and fishes in which a parent broods externally fertilized eggs or larvae in the mouth, stomach, on the dorsum, or in a body pouch (Greven, 2011; Wake, in press), the term "pseudoviviparity" can be applied (Blackburn, 1999a, in press).

A separate distinction is based on the sources of nutrients for embryonic development. In "lecithotrophy" the ovum's own yolk provides nutrients for development, whereas in "matrotrophy," extravitelline nutrients are provided to embryos/fetuses by the pregnant female during their gestation in her reproductive tract (Wourms, 1981; Blackburn, 1992, 1994; Mess et al., 2003; Stewart, 2013). Lecithotrophy and matrotrophy represent extremes of a continuum, because in many viviparous species, the embryos derive nutrients from their own yolk as well as other (postovulatory) maternal sources (Wourms et al., 1988; Stewart, 1992, 2013; Marsh-Matthews, 2011). "Placentotrophy" is a form of matrotrophy that involves a placenta—defined as an "intimate apposition of the fetal organs to the maternal or paternal tissues for physiological exchange" (Mossman, 1937). Other forms of matrotrophy include "histotrophy" (embryonic absorption of maternal nutrients); "oophagy" (ingestion of sibling yolks); "embryophagy" (cannibalism of sibling embryos, sometimes called "adelphophagy"); and "matrophagy" (ingestion of maternal tissues) (Wourms, 1981; Blackburn et al., 1985; Wourms et al., 1988; Blackburn, in press).

Implications for Evolution

The fact that viviparity and matrotrophy have evolved convergently in diverse animal lineages has been widely- recognized for more than a century (Haacke, 1885; Giacomini, 1906; Gadow, 1910; Kerr, 1919). Phylogenetic analyses of squamate reptiles in the 1980s concluded that viviparity has evolved at least 90 times (Blackburn, 1982, 1985; Shine, 1985), a number that has increased to more than 115 origins as further data have accumulated (Blackburn, 1999b, 2000b, in press). Multiple origins also have been defined in fishes (Dulvy and Reynolds, 1997; Blackburn, 2005; cf. Musick and Ellis, 2005), caecilian amphibians (Gower et al., 2008), and extinct reptiles (Organ et al., 2009; Blackburn and Sidor, in press). An analysis published in this virtual issue of *Journal of Morphology* has identified more than 150 evolutionary origins of vertebrate viviparity and 33 separate origins of matrotrophy (Blackburn, in press); it also documented multiple origins of each of the major types of matrotrophy. The convergent evolution of viviparity and specializations for fetal nutrition raises significant questions about the roles of selective pressures, constraints, adaptation, exaptation, and other factors that have affected the evolution of these patterns (Shine, 1985; Wake, 1982, 1985; Wourms et al., 1988; Blackburn, 2006, in press). Morphology is in an excellent position to address such questions.

THE ROLE OF MORPHOLOGY

Functional Issues

For viviparous embryos, development within the maternal reproductive tract (oviduct, uterus, or ovary) confers both difficulties and potential means for their resolution. The most immediate problem facing a viviparous embryo is exchange of respiratory gases, given the hypoxic nature of the female reproductive tract. Many types of specializations facilitate maternal-fetal gas exchange, including fetal membranes (such as the chorioallantois and yolk sac), embryonic gills, fins, tail, skin, and pericardial sac, and on the maternal side, modifications to lining of the oviduct, uterus, and ovary. Squamates face an additional functional problem, in that viviparity requires evolutionary loss of the eggshell, which thereby deprives the embryo of a significant source of calcium (Stewart and Ecay, 2010; Stewart, 2013; Stewart and Blackburn, 2014). Physiological difficulties aside, viviparity also opens opportunities for supplementation of yolk supplies with maternal nutrients, given the proximity of fetal and maternal tissues.

Morphological approaches are essential in studies of mechanisms by which pregnant females sustain their developing embryos. In cases of matrotrophy, aspects to be analyzed include histological and cytological specializations for nutrient synthesis, secretion, and embryonic uptake; the histochemical nature of maternally supplied nutrients; the developmental origins and morphogenesis of specializations for matrotrophy; and the timing during gestation of maternal—fetal nutrient transfer. Features that enhance maternal—fetal gas exchange (such as increased vascularity and decreased diffusion distances) can likewise be considered. Structural analysis also can lead to new, testable functional hypotheses, such as the inference of sodium-coupled water transport across the yolk sac placenta of viviparous snakes (Blackburn et al., 2002). Relevant techniques include histology, scanning, and transmission electron microscopy, histochemistry, and confocal microscopy, in conjunction with physiological and biochemical methods that have become subsumed within contemporary morphology. The papers featured in this virtual issue of *Journal of Morphology* collectively offer a powerful demonstration of the value of such methods.

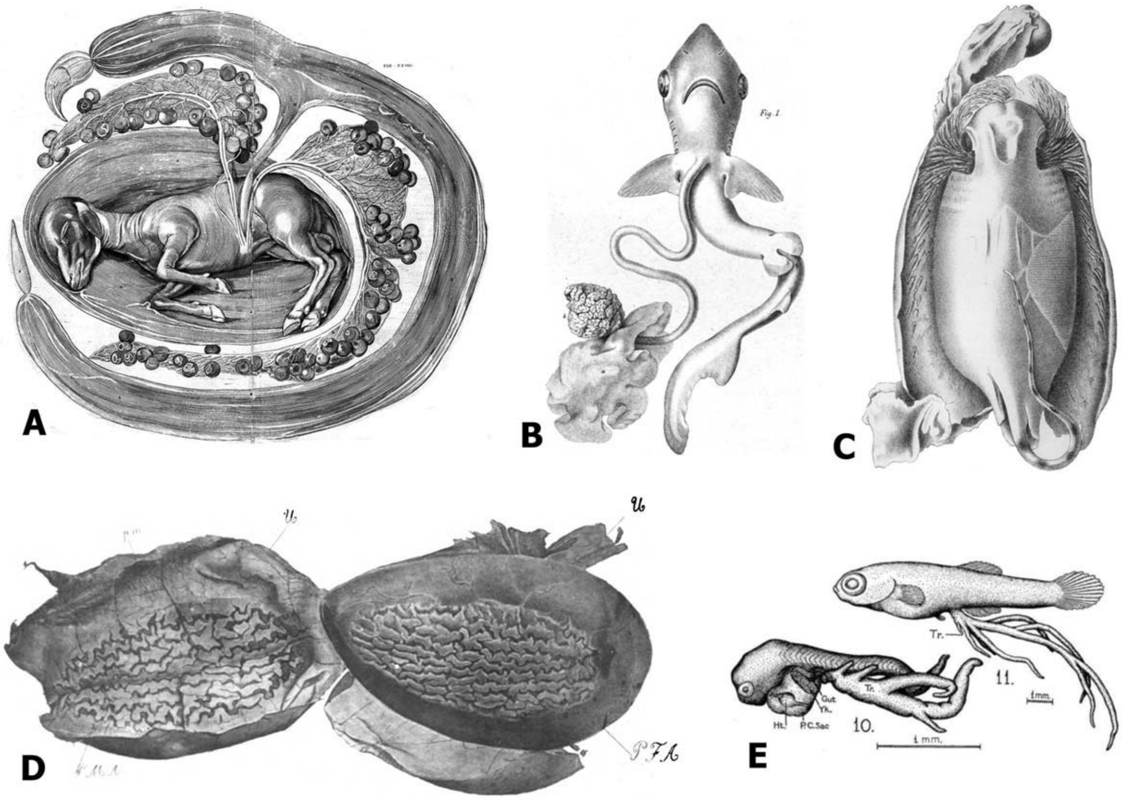

Fig. 1. Diagrams from classic papers on specilizations for fetal nutrition. A) Goat placenta, from Fabricius's 1604 *De Formato Foetu*. B) Yolk sac placenta and fetus of the dogfish *Mustelus canis* (from Müller [Abhandl Aka Wiss Berlin, 1842, 27:187–257]). C) Pregnant uterus of a batoid ray, showing nutritive trophonemata that extending into the fetal gill slits (from Wood-Mason and Alcock [Proc Roy Soc B, 1891, 49:359–367]). D) Chorioallantoic placenta of the lizard *Chalcides chalcides*, showing the inside of the ridged uterus (left) and external surface of the chorion (right) (from Giacomini [1891a, Archiv Ital Biol 16:332–359]). E) Nutritive trophotaeniae in embryos of a goodeid fish (Reproduced with permission from Turner [1940d, J Morphol 67:271–289]).

Evolutionary Morphology

Morphological studies have been central to reconstructions of the evolution of viviparity and matrotrophy; in fact both of these patterns can be recognized based on anatomical criteria. Among the evolutionary aspects that morphology can address are the nature and extent of convergences; the roles of exaptation, constraint, and heterochrony; and the historical transformations that have led to particular reproductive specializations (Blackburn, in press). For instance, morphological analysis has revealed the roles of heterochrony in evolution of specializations for matrotrophy in salamanders (Dopazo and Alberch, 1994; Buckley et al., 2007), teleosts (Skov et al., 2007, 2010), and lizards (Stewart and Thompson, 2009a, 2009b; Leal and Ramírez-Pinilla, 2010). Likewise, morphological data are central to attempts to reconstruct the evolutionary history of mammalian placentas (Freyer et al., 2003; Mess and Carter, 2006, 2007; Wildman et al., 2006; Carter and Mess, 2007; Carter and Enders, 2013). Similarly, detailed information on trophotaenial structure and function in goodeid fishes is necessary for reconstruction of their evolutionary history (Doadrio and Domínguez, 2004). When interpreted phylogenetically, morphological data also can facilitate quantitative evolutionary reconstructions. For example, comparative analysis has revealed that embryonic respiratory structures have been recruited evolutionarily for nutrient uptake in nearly two-thirds of the 33 clades of matrotrophic vertebrates, and has allowed estimates of how frequently each type of matrotrophy has originated (Blackburn, in press).

HISTORICAL BACKGROUND

The study of specializations by which pregnant animals maintain their embryos extends back nearly 2400 years (Figs. 1 and 2). In his *Historia Animalium*, Aristotle provided the first descriptions of the placentas of mammals and sharks and recognized their commonalities. During the 16th and 17th centuries, several prominent works described and illustrated placental structure in humans and other eutherian mammals by such authors as Jacob Rueff, Giulio Aranzi, Andreas

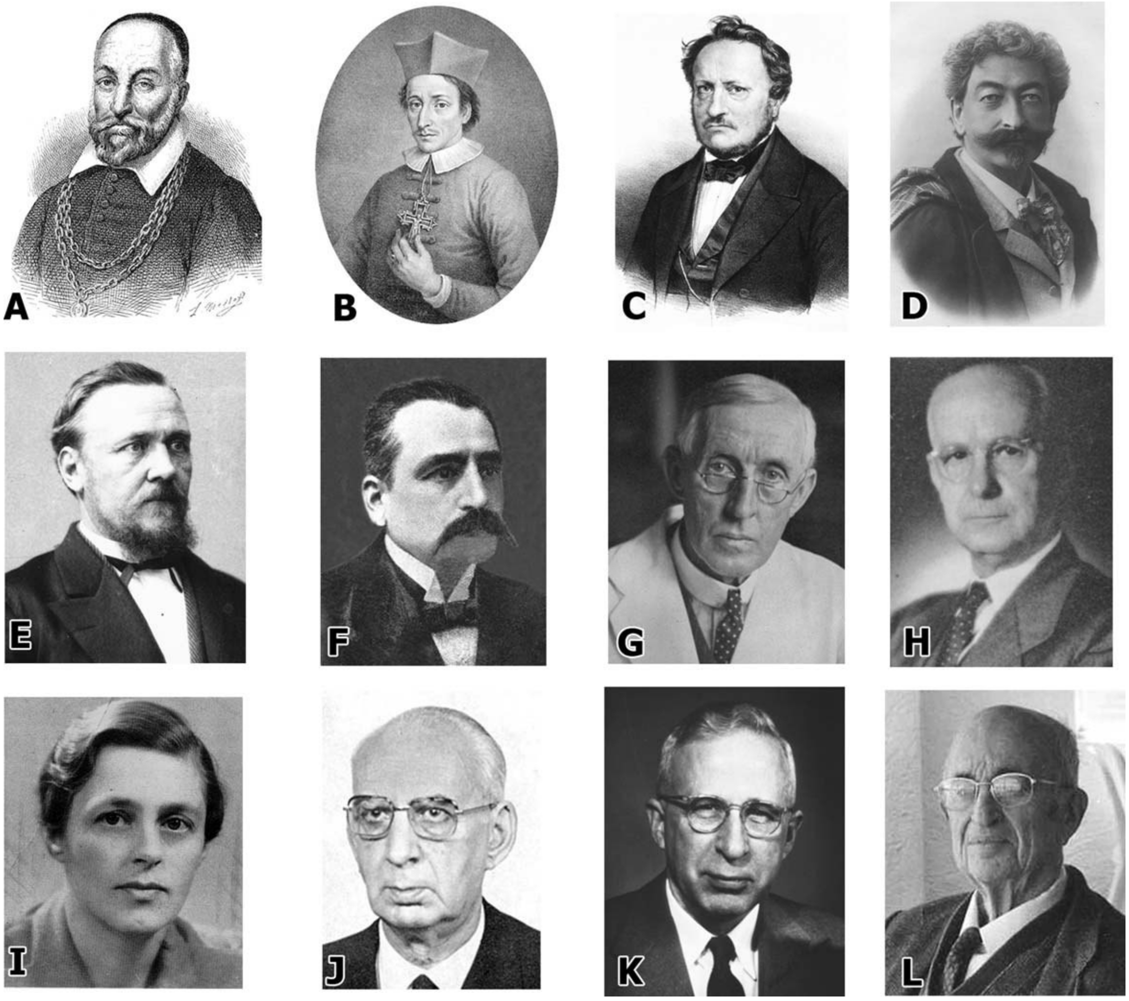

Fig. 2. Eminent scientists who have contributed significantly to our understanding of morphological specializations for fetal nutrition (see text). A) Hieronymus Fabricius (1537–1619). B) Nicolas Steno (1638–1686). C) Johannes Peter Müller (1801–1858). D) Emil Selenka (1842–1902). E) Hans Strahl (1857–1920). F) Ercole Giacomini (1864–1944). G) J.P. Hill (1873–1954). H) Clarence L Turner (1890–1969) (Reproduced with permission from Turner [Bios 1954, 25:2–34]). I) Hazel Claire Weekes (1903–1990) (Reproduced with permission from Mess et al. [J Morphol 2003, 274:557–569]). J) Silvio Ranzi (1902–1996). K) Harland W. Mossman (1891–1991). L) Maurice Panigel (1926–2005).

Vesalius, and Walter Needham (Steven, 1975; Longo and Reynolds, 2010). Of these works, Fabricius' 1604 *De Formato Foetu* is notable for the outstanding quality and detail of its illustrations (Adelmann, 1942; Fig. 1A). While documenting structural diversity among mammalian placentas, such early works were unable to address the most basic of functional issues, such as whether fetal and maternal blood mixed and how placentas maintained developing embryos (De Witt, 1959). Controversies continued into the 19th century and were only resolved with studies of placental physiology and the application of microscopic techniques (Longo, 2013).

During the Renaissance and its aftermath, recognition of specializations for fetal nutrition in other vertebrates lagged behind work on eutherian mammals. However, following observations on chondrichthyan viviparity by Rondelet and Belon during the 1500s (Wourms and Demski, 1993), Fabricius (Fig. 2A) described and illustrated the embryos and uterus of a pregnant (though aplacental) shark (Adelmann, 1942). In an early work on viviparous teleosts, Schoenveld (1624) correctly inferred that embryos of the eelpout *Zoarces viviparus* obtain nutrients during gestation by imbibing ovarian secretions. Lorenzini (1678) observed oviductal trophonemata in the electric ray *Torpedo*, structures that he inferred to secrete nutrients that are ingested by the embryos. These two sources may be the first to recognize viviparous histophagy. In 1673, the Danish anatomist Nicolas Steno (Fig. 2B) published a description of the yolk sac placenta in the shark *Mustelus canis;*

he also distinguished between placental and aplacental viviparity (Steno, 1673; see Wourms, 1997; Kardet and Maquet, 2012). Steno's inferences of placentation remained controversial until corroborated nearly two centuries later by Johannes Müller (Fig. 2C), who detailed descriptions of the yolk sac placentas of *M. canis* and *Prionace glauca* (Müller, 1842; Fig. 1B).

During the 19th century, specializations for fetal sustenance received increased attention in diverse vertebrates (Steven, 1975; Wourms, 1997; Longo and Reynolds, 2010; Longo, 2013). Although much of this early work focused on therian mammals, the first description of a lizard placenta was published at this time, based on macroscopic observations (Studiati, 1855). Viviparity had long been recognized in the urodele genus *Salamandra* (Adler, 2003) and fetal maintenance via oophagy was documented in *S. atra* in the 1830s (Francis, 1934). Among specializations for matrotrophy described in teleosts were the absorptive abdominal "trophoderm" of *Anableps* embryos (Wyman, 1854) and the hypertrophied hindgut of surf perch embryos (Ryder, 1886), which absorbs ingested secretions of the ovary. Various specializations for matrotrophy also were described in chondrichthyans, including absorptive appendiculae of the umbilical cord of a shark (Alcock, 1890) and trophonemata in a batoid ray (Wood-Mason and Alcock, 1891). The latter are secretory projections of the uterine mucosa that extend into the fetal gill slits (Fig. 1C), an arrangement later termed the "branchial placenta" (Wourms et al., 1988).

The development of paraffin-section histology by the 1870s stimulated numerous investigations into the microscopic anatomy of placental structures, especially those of mammals. Among the early pioneers of placental morphology and development in mammals were Emil Selenka (Fig. 2D), Ambrosius Hubrecht, Hans Strahl (Fig. 2E), Mathias Duval, Charles Sedgwick Minot, Otto Grosser, and J.P. Hill (Fig. 2G). (For historical information, see Hubrecht, 1903; Morse, 1920; Lubosch, 1922; Watson, 1955; Boyd and Hamilton, 1970; Carter, 1999; Mess et al., 2003; Carter and Mess, 2010; Longo and Reynolds, 2010; Longo, 2013; Pijnenborg and Vercruysse, 2004, 2006, 2013). Early mammalian work also included microscopic studies on marsupials (Osborn, 1883, 1887; Caldwell, 1884; Semon, 1894; Hill, 1898, 1900), as well as comprehensive classifications of placental structure by Hans Strahl (1906) and Otto Grosser (1909) (for modern perspectives see Kaufman, 1992; Carter and Mess, 2010). Meanwhile, growing information about placental diversity was used to infer phylogenetic relationships in therian mammals (Huxley, 1864, 1890; Haeckel, 1866, 1883; see Pijnenborg and Vercruysse, 2004). Research published near the turn of the 20th century included a remarkable series of monographs by Ercole Giacomini (1891a, 1891b, 1893, 1906; Fig. 2F) on placental and oviductal histology in (nonavian) reptiles. Fortuitously, Giacomini's placental studies focused on two species of the lizard genus *Chalcides* that differ markedly in the degree of placentotrophy, a difference reflected in cytological specializations for nutrient transfer (Yaron, 1985; Ghiara et al., 1987; Blackburn, 1993a; Fig. 1D). Giacomini recognized parallels between placentation in eutherian mammals and reptiles, and established the importance of live-bearing squamates for comparative studies on viviparity and embryology.

The 1920s and 1930s heralded a "golden age" of morphological research on viviparity. Among many other works, this period yielded Clarence Turner's (Fig. 2H) extensive studies on specializations for matrotrophy in viviparous teleosts (1933a, 1933b, 1936, 1937, 1938a, b, 1940a, b, c, d; Fig. 1E). It also included Claire Weekes' (Fig. 2I) groundbreaking work on viviparity and placentation in lizards and snakes (Weekes, 1927, 1929, 1930, 1934, 1935); ten Cate-Hoedemaker's (1933) detailed account of placentas in a lizard and a shark; Hanni Hrabowski's (1926) analysis of fetal membrane development in lizards (see Stewart et al., 2004); and Silvio Ranzi's (Fig. 2J) comprehensive research on viviparity and matrotrophy in chondrichthyans (Ranzi, 1932, 1934). This decade also yielded Harland Mossman's (Fig. 2K) famous 1937 monograph on the mammal placenta, a work exceeded in scope 50 years later by his magnum opus, *Vertebrate Fetal Membranes* (Mossman, 1937, 1987, 1991). Anatomical research continued into the 1950s, accompanied by physiological and experimental approaches. Comprehensive compilations of what was known about mammalian placentation were published by Amoroso (1952) and Starck (1959). Research by Maurice Panigel (Fig. 2L) on placentation and gestation in the lizard *Zootoca vivipara* provides a good example of the growing integration of morphological and physiological methods (Panigel, 1951a, b, c, 1953, 1956).

Development of the techniques of electron microscopy (EM) stimulated an outpouring of research on specializations for fetal maintenance. Electron microscopy revealed new details of placental interfaces along with subcellular features indicative of maternal secretion and fetal absorption. First applied to mammalian placentas in the 1950s (Dempsey, 1953; Boyd and Hughes, 1954; Dempsey et al., 1955; Wislocki and Dempsey, 1955), this instrumentation was adopted over the following decades in numerous studies on mammals (for reviews see Starck, 1959; Ramsey, 1982; Mossman, 1987; Wooding and Burton, 2008; Carter and Enders, 2013). In the 1960s and 1970s, electron microscopy was first applied to chondrichthyan placentas (Jollie and Jollie, 1967a, b) and to teleost specializations for matrotrophy

(Jollie and Jollie, 1964a, b; Mendoza, 1972; Dobbs, 1975; Wourms and Cohen, 1975). Electron microscopy was extensively used in piscine studies in the 1980s and 1990s (e.g., Hamlett et al., 1985a, b, c, d, 1996; Knight et al., 1985; Lombardi and Wourms, 1985a, b, c, 1988; Schindler and de Vries, 1986, 1987, 1988a, b; Schindler, 1990; Schindler and Kujat, 1990; Grove and Wourms, 1991, 1994; Schindler and Greven, 1992; Hollenberg and Wourms, 1994, 1995). Ultrastructural studies on amphibian adaptations for viviparity also proliferated during this period (Greven, 1977, 1980a, b, 1998; Wake, 1980; Greven and Rüterbories, 1984). As for research on reptiles, despite an early ultrastructural study (Hoffman, 1970), three decades elapsed before EM was again applied to squamate placentation (Blackburn et al., 2002; Blackburn and Vitt, 2002). However, several ultrastructural studies have since accumulated (for reviews see Blackburn and Stewart, 2011; Stewart and Blackburn, 2014).

The 1980s through the present arguably represent a second "golden age" of research on morphological specializations for viviparity and matrotrophy. This period coincided with a rapid growth of interest in vertebrate viviparity that extended throughout the biological sub-disciplines. As evidence of the upsurge of interest, 13 international symposia have been held on aspects of viviparity and fetal nutrition since 1990 (Blackburn, in press). More morphological papers on these phenomena have been published during this time period than in all of previous history. Enumerating such papers herein is not feasible, but many are listed in recent reviews (Wourms et al., 1988; Hamlett, 2005; Hamlett et al., 2005; Greven, 2011; Blackburn and Stewart, 2011; Carter, 2012; Carter and Enders, 2013; Stewart, 2013; Stewart and Blackburn, 2014; Wake, in press; Blackburn, in press).

Retrospective

A significant question in the history of science is whether progress is driven chiefly by technological innovation, conceptual advances, or the efforts of a few influential individuals. With respect to our understanding of viviparous maintenance of embryos, all three parameters clearly have played major roles. Each successive development of microscopic techniques (e.g., histological sectioning and staining, electron microscopy, immunocytochemistry) answered many questions yet opened fresh avenues of research. Conceptual advances also contributed, such as the development of evolutionary ideas, the application of phylogenetic analyses to morphological diversity, and recognition of the roles of heterochrony and exaptation in the generation of novel phenotypes.

Nevertheless, the impact of key individuals in particular time frames ought not to be underestimated. Outside of the realm of eutherian mammals (which have received attention from numerous researchers), much of our understanding of specializations for fetal nutrition stems from the influence of a small number of individuals. Among them are the pioneers of the 1930s and their forerunners at the turn of the last century, as well as their more recent counterparts. As a result, progress on particular viviparous taxa has waxed and waned with the careers of a handful of individuals. For example, Claire Weekes' enormously fruitful decade of contributions (1925–1935) was followed by a half century that yielded few papers on squamate placentation, some of which were of questionable quality (for reviews, see Blackburn, 1993b, 1998; Stewart, 1993). Likewise, after an extended period of remarkable productivity marked by work of the late John P. Wourms (Ptacek, 2005), William C. Hamlett, and their colleagues and students, morphological research on piscine matrotrophy appears to be experiencing a similar lull (however, see Schindler, in press; Kwan et al., in press; and Uribe et al., 2014). As another example, recognition of the marsupial reproductive pattern as "alternative" (rather than "inferior") to that of eutherians (Renfree, 1981, 1983, 2010; Tyndale-Biscoe and Renfree, 1987) helped stimulate more than three decades of fruitful research on these animals. These situations emphasize the extraordinary impact that a few individuals can have on the field. Given how little we know (as compared to what remains to be discovered), the question arises as to which members of the next generation of scientists will accept the challenge of applying morphological and physiological techniques to the many significant questions that remain unanswered.

ROLE OF THE JOURNAL OF MORPHOLOGY

Papers and monographs on specializations for the viviparous maintenance of embryos have chiefly appeared in the major anatomical journals. The *Journal of Morphology* has played a significant role in publishing such papers. Listed in Tables 1 and 2 are >140 papers on this topic published by this journal since 1887. The contributed papers are broad in taxonomic scope and include work on each of the major groups of viviparous vertebrates (squamates, teleosts, selachians, batoids, therians, and lissamphibians), as well as various viviparous and pseudoviviparous invertebrates. They likewise reflect a host of morphological techniques as well as diverse functional and evolutionary hypotheses.

Among papers that have appeared in the *Journal of Morphology* are several "firsts" that warrant mention. These include the following: one of the

TABLE 1. Papers on specializations for viviparity and fetal maintenance published by the Journal of Morphology (1887–2015).

Papers	Specializations	Taxa
Chondrichthyans		
Castro and Wourms, 1993	Placenta	*Rhizoprionodon* (Carcharhinidae)
Fishelson and Baranes, 1998	Placenta	*Iago omanensis* (Triakidae)
Schlernitzauer and Gilbert, 1966	Placenta	*Sphyrna tiburo* (Sphyrnidae)
Storrie et al., 2009*	Uterus, matrotrophy	*Mustelus antarcticus* (Triakidae)
Tewinkel, 1943	Yolk sac, fetal nutrition	*Squalus acanthias* (Squalidae)
Teleost fishes		
Campuzano-Caballero and Uribe, 2014	Gonoduct	*Poecilia reticulata* (Poeciliidae)
Grove and Wourms, 1991	Follicular placenta	*Heterandria formosa* (Poeciliidae)
Grove and Wourms, 1994	Follicular placenta	*Heterandria formosa* (Poeciliidae)
Hollenberg and Wourms, 1994	Trophotaeniae, matrotrophy	Goodeidae
Jollie and Jollie, 1964a	Pregnant ovarian follicle	*Lebistes reticulatus* (Poeciliidae)
Jollie and Jollie, 1964b	Follicular placenta	*Lebistes reticulatus* (Poeciliidae)
Kokkala and Wourms, 1994	Trophotaenial placenta	Goodeidae
Knight et al., 1985	Follicular placenta, development	*Anableps* (Anablepidae)
Kwan et al., in press	Follicular placenta	*Poeciliopsis* (Poeciliidae)
Lombardi and Wourms, 1985a	Trophotaenial placenta	*Ameca splendens* (Goodeidae)
Lombardi and Wourms, 1985b*	Trophotaenial placenta	*Ameca splendens* (Goodeidae)
Lombardi and Wourms, 1988	Placental function, matrotrophy	*Ameca splendens* (Goodeidae)
Meisner and Burns, 1997	Specializations for matrotrophy	Hemiramphidae
Mendoza, 1937	Trophotaenial resorption	Goodeidae
Mendoza, 1956	Trophotaeniae and ovary	*Hubbsina turneri* (Goodeidae)
Mendoza, 1958	Specializations for matrotrophy	*Goodea luitpoldii* (Goodeidae)
Mendoza, 1972	Trophotaeniae	*Xenotoca eiseni* (Goodeidae)
Parenti et al., 2010	Reproductive histology	*Tomeurus gracilis* (Poeciliidae)
Schindler and de Vries, 1986	Trophotaeniae	*Girardinichthys viviparus* (Goodeidae)
Schindler and de Vries, 1988a	Specializations for matrotrophy	*Jenynsia lineata* (Anablepidae)
Turner, 1933a	Viviparity	Goodeidae
Turner, 1936	Trophotaeniae	*Parabrotula dentiens* (Brotulidae)
Turner, 1937	Trophotaeniae	Goodeidae
Turner, 1938a	Ovarian viviparity, matrotrophy	*Cymatogaster aggregatus* (Embiotocidae)
Turner, 1938b	Specializations for matrotrophy	*Anableps anableps*
Turner, 1940a	Specializations for matrotrophy	*Jenynsia* (Anablepidae)
Turner, 1940b	Specializations for matrotrophy	Anablepidae
Turner, 1940c	Specializations for matrotrophy	Poeciliidae
Turner, 1940d	Specializations for matrotrophy	Goodeidae
Turner, 1950	Specializations for fertilization	*Anableps anableps*
Uribe and Grier, 2011	Matrotrophic oogenesis	*Heterandria formosa* (Poeciliidae)
Wourms and Cohen, 1975	Trophotaeniae	*Oligopus* (Bythitidae)
Amphibians		
del Pino and Escobar, 1981	Pseudoviviparous development	*Gastrotheca riobambae* (Anura: Hylidae)
Greven and Richter, 2009	Pseudoviviparous development	*Pipa carvalhoi* (Anura: Pipidae)
Wake, 1968	Urogenital system	caecilians
Wake, 1976*	Fetal dentition used in matrophagy	viviparous caecilians
Wake, 1980	Fetal dentition	*Dermophis mexicanus* (Gymnophiona)
Squamate reptiles		
Adams et al., 2005	Pregnant uterus	*Pseudemoia entrecasteauxii* (Scincidae)
Adams et al., 2007a	Pregnant uterus	*Eulamprus tympanum* (Scincidae)
Adams et al., 2007b	Pregnant uterus	*Lerista bougainvillii* (Scincidae)
Anderson et al., 2011	Placental ultrastructure (SEM)	*Sceloporus jarrovi* (Phrynosomatidae)
Blackburn, 1993a	Placentation, matrotrophy	*Chalcides chalcides* (Scincidae)
Blackburn and Callard, 1997	Placental development	*Chalcides chalcides* (Scincidae)
Blackburn and Lorenz, 2003a*	Chorioallantoic placentation	*Thamnophis* (Colubridae)
Blackburn and Lorenz, 2003b	Yolk sac placentation	*Thamnophis* (Colubridae)
Blackburn and Vitt, 2002	Placentation, matrotrophy	*Mabuya heathi* (Scincidae)
Blackburn et al., 1998	Pregnancy, spontaneous abortion	*Chalcides chalcides* (Scincidae)
Blackburn et al., 2002	Placental ultrastructure	*Thamnophis* (Colubridae)
Blackburn et al., 2003	Pregnancy, spontaneous abortion	*Pseudemoia pagenstecheri* (Scincidae)
Blackburn et al., 2009	Placental ultrastructure	*Storeria dekayi* (Colubridae)
Blackburn et al., 2010	Placental ultrastructure (TEM)	*Sceloporus jarrovi* (Phrynosomatidae)
Corso et al., 2000	Pregnant uterus	*Chalcides ocellatus* (Scincidae)
Crocco et al., 2008	Placentation	*Liolaemus elongatus* (Liolaemidae)
Flemming and Branch, 2001	Placentation, matrotrophy	*Eumecia anchietae* (Scincidae)
Girling et al., 1997	Oviduct	*Hoplodactylus maculatus* (Gekkonidae)
Gómez and Ramírez-Pinilla, 2004	Matrotrophic oogenesis	*Mabuya mabouya* (Scincidae)

Table 1. (continued).

Papers	Specializations	Taxa
Guillette, 1992	Oviduct	*Sphenomorphus fragilis* (Scincidae)
Guillette and Jones, 1985	Placenta	*Sceloporus aeneus* (Phrynosomatidae)
Hernández-Franyutti et al., 2005	Matrotrophic oogenesis	*Mabuya brachypoda* (Scincidae)
Heulin et al., 2002	Eggshell (viviparous)	*Zootoca vivipara* (Lacertidae)
Heulin et al., 2005	Uterine glands	*Zootoca vivipara* (Lacertidae)
Hoffman, 1970	Placentation	*Thamnophis sirtalis* (Colubridae)
Hosie et al., 2003	Uterus	*Eulamprus tympanum* (Scincidae)
Jerez and Ramírez-Pinilla, 2001*	Placentation	*Mabuya mabouya* (Scincidae)
Jerez and Ramírez-Pinilla, 2003	Placental development	*Mabuya mabouya* (Scincidae)
Knight and Blackburn, 2008	Fetal membranes (oviparous)	*Pantherophis guttatus* (Colubridae)
Qualls, 1996	Eggshell (viviparous)	*Lerista bougainvillii* (Scincidae)
Ramírez-Pinilla et al., 2006	Placentation	*Mabuya* (Scincidae)
Sever et al., 2000	Oviduct	*Seminatrix pygaea* (Colubridae)
Siegel and Sever, 2008	Oviduct	*Agkistrodon piscivorus* (Viperidae)
Stewart, 1985	Placentation	*Elgaria coerulea* (Anguidae)
Stewart, 1990	Placentation	*Virginia striatula* (Colubridae)
Stewart and Brasch, 2003	Placentation	*Virginia striatula* (Colubridae)
Stewart and Florian, 2004	Fetal membranes (oviparous)	*Eumeces fasciatus* (Scincidae)
Stewart and Thompson, 1994	Placentation	*Niveoscincus metallicus* (Scincidae)
Stewart and Thompson, 1996*	Placentation	*Pseudemoia entrecasteauxii* (Scincidae)
Stewart and Thompson, 2004	Placentation	*Niveoscincus ocellatus* (Scincidae)
Stewart and Thompson, 2009a	Placental development	*Niveoscincus coventryi* (Scincidae)
Stewart et al., 2010	Uterine and eggshell histochemistry	*Saiphos equalis* (Scincidae)
Uribe-Aranzábal et al., 2006	Oviduct, matrotrophy	*Mabuya brachypoda* (Scincidae)
Vieira et al., 2010	Ovarian ultrastructure	*Mabuya* (Scincidae)
Villagrán et al., 2005	Placentation	*Sceloporus mucronatus* (Phrynosomatidae)
Mammals		
Blackburn et al., 1988	Placental evolution, viviparity	Therian mammals
Blackburn et al., 1989	Placental development, giant cells	*Sylvilagus* (rabbit)
Bridgman, 1948a	Placental development	*Rattus norvegicus* (rat)
Bridgman, 1948b	Placental development	*Rattus norvegicus*
Bryden et al., 1972	Fetal membranes; embryogenesis	*Ovis aries* (sheep)
Calarco and Moyer, 1966	Yolk sac development	*Mus musculus* (mouse)
Carvalho et al., 2006	Placental giant cells	*Bubalus bubalis* (water buffalo)
Cunha et al., 2003	Female reproductive tract	*Crocuta crocuta* (hyena)
Dudley et al., 2015	Uterine cytology	*Sminthopsis crassicaudata* (fat-tailed dunnart)
Faria and Bevilacqua, 1995	Trophoblast invasion	*Calomys callosus* (vesper mouse)
Ferro and Bevilacqua, 1994	Ovo-implantation	*Calomys callosus*
Franklin and Brent, 1964	Placental vasculature	*Rattus norvegicus*
Fujimura, 1921	Placental secretion	human
Fuller et al., 1994	Trophoblast invasion	*Mesocricetus auratus* (golden hamster)
Gabie, 1959*	Embryogenesis	*Eremitalpa granti* (golden mole)
Gabie, 1960	Placentation	*Eremitalpa granti*
Gopalakrishna, 1958	Fetal membranes	Microchiropteran bats
Hartman, 1928	Development	*Didelphis virginiana* (opossum)
Heuser, 1940	Ovo-implantation	*Pan troglodytes* (chimpanzee)
Huber, 1915a	Blastula formation	*Rattus norvegicus* (rat)
Huber, 1915b	Early embryogenesis	*Rattus norvegicus*
Lillegraven, 1985	Embryogenesis, evolution	Therian mammals
Maris et al., 1988	Ovo-implantation, giant cells	*Mus musculus* (mouse)
Meyer, 1919	Placental macrophages	human
Minot, 1889	Placentation	human; rabbit
Newman and Patterson, 1910	Development, placentation	*Dasypus novemcinctus* (armadillo)
Öner et al., 2006	Ovo-implantation	*Rattus norvegicus*
Orsini, 1957	Placental vasculature	*Mesocricetus auratus* (golden hamster)
Osborn, 1887	Placentation	*Didelphis virginiana* (opossum)
Patterson, 1913	Embryogenesis	*Dasypus novemcinctus* (armadillo)
Schooley, 1934	Embryogenesis	Sciuridae (squirrels)
Tibbitts and Hillemann, 1959	Placentation	*Chinchilla lanigera* (chinchilla)
Wislocki, 1928	Placentation	*Bradypus choloepus* (sloth)
Invertebrates		
Ben-Ami and Hodgson, 2005	Brood pouch	*Melanoides* (trumpet snail; Gastropoda)
Berrill, 1948	Viviparous development	ascidians (Urochordata)
Berrill, 1950	Viviparous development	*Salpa* (tunicate; Urochordata)

Table 1. (continued).

Papers	Specializations	Taxa
Campiglia and Walker, 1995	Placenta, development	*Peripatus* (velvet worm; Onychophora)
Farley, 1998	Embryogenesis, matrotrophy	*Paruroctonus* (scorpion; Arachnidae)
Hagan, 1931	Viviparous development	*Hesperoctenes* (polyctenid insects)
Mukai, 1977	Brood pouch formation	Botryllidae (ascidians; Urochordata)
Mukai et al., 1987	Viviparous development	*Botrylloides* (ascidians; Urochordata)
Smith, 1950	Viviparous development	*Alitta* (sandworm; Annelida, Polychaeta)
Woollacott and Zimmer, 1975	Matrotrophy, placentation	*Bugula* (tufted bryozoans; Bryozoa)

More recent papers are listed in Table 2.
Asterisks indicate papers currently being made available online on a complimentary basis.

TABLE 2. Contents of the online virtual issue: papers related to viviparity and specializations for fetal maintenance. Asterisks indicate papers currently being made available online on a complimentary basis.

Papers	Topic	Taxa
Blackburn, 2014*	Review, evolutionary morphology	Viviparous vertebrates
Blackburn and Flemming, 2012	Ovo-implantation, placentation	*Trachylepis ivensii* (Squamata; Scincidae)
Carter and Mess, 2013	Placental morphology and evolution	South American mammals
Ferner et al., 2014	Placental morphology and evolution	Eutherian mammals
Laird et al., 2014	Uterine cytology	*Sminthopsis crassicaudata* (Marsupialia: Dasyuridae)
Ramírez-Pinilla et al., 2012	Placental structure, angiogenesis	*Niveoscincus coventryi* (Squamata; Scincidae)
Schindler, in press	Placental structure and function	Goodeid fishes (Teleostei: Goodeidae)
Stewart, 2013*	Review: evolutionary morphology	Viviparous squamate reptiles
Stewart et al., 2012	Fetal membrane development	*Oligosoma lichenigerum* (Squamata; Scincidae)
Stinnett et al., 2012	Placental development, calcium transport, calcium transport	*Pseudemoia pagenstecheri* (Squamata; Scincidae)
Uribe et al., 2014	Branchial placenta histology	*Ilyodon whitei* (Teleostei: Goodeidae)
Wake, in press*	Review: evolutionary morphology	Live-bearing amphibians

earliest accounts of a yolk sac placenta in a marsupial (Osborn, 1887); details of the only known case of invasive ovo-implantation into the uterus of a viviparous sauropsid (Blackburn and Flemming, 2012); the first broad survey of gonadal morphology in caecilians (Wake, 1968); the first studies of sauropsid placentas to use transmission EM (Hoffman, 1970) and scanning EM (Blackburn et al., 2002; Blackburn and Vitt, 2002); the first ultrastructural studies on teleosts of the follicular placenta (Jollie and Jollie, 1964b), the branchial placenta (Schindler and de Vries, 1988a, 1988b), and fetal trophotaeniae (Mendoza, 1972; Wourms and Cohen, 1975); and the only microscopic study of the gonoduct of a viviparous teleost (Campuzano-Caballero and Uribe, 2014). In addition, *Journal of Morphology* has published all of the studies on placental morphology in snakes that have appeared since the 1960s (7 papers); accounts of larval development and matrotrophy in live-bearing invertebrates of six phyla (10 papers); analyses of specializations for placentotrophy in all six of the known clades of matrotrophic lizards (16 papers); and numerous works on morphological specializations for matrotrophy in teleosts (30 papers), including most of the anatomical work in this area published by such historically important figures as John P. Wourms (Ptacek, 2005), Clarence L. Turner (Uribe, 2005), and Guillermo Mendoza (Grier, 2005) (see Tables 1 and 2).

The Virtual Issue of *Journal of Morphology*

In view of its active role historically and recently, the *Journal of Morphology* is an ideal venue for a compilation of papers resulting from the ICVM symposium along with other recent works. The 12 papers making up this virtual issue of the journal are listed in Table 2. All stem from work published in the past three years. They include studies on viviparous squamates, mammals, teleost fishes, and amphibians, with a taxonomic distribution that parallels the output of recent research in this area. These papers employ the following techniques: paraffin- and resin- section histology, transmission electron microscopy, scanning EM, confocal microscopy, histochemistry, immunocytochemistry, freeze- fracture techniques, and morphometric analysis, in conjunction with gel electrophoresis, *in vitro* manipulations, and other physiological and biochemical techniques. They also use phylogenetic analysis as a means of generating hypotheses and interpreting data. Thus, these papers draw upon the full spectrum of methods used in contemporary morphology and integrative biology. Among the papers are three comprehensive reviews solicited for this special issue of the journal. One such review (Stewart, 2013) offers insight into early stages in the development of viviparity and placentation in squamates. A second review summarizes the extensive work done on live- bearing amphibians (Wake, in press), and a third one analyzes the overall evolution of specializations for matrotrophy in viviparous vertebrates (Blackburn, in press).

As noted above, the publisher of *Journal of Morphology*, John Wiley and Sons, is making available free of charge a number of papers related to specializations for fetal maintenance in viviparous vertebrates. These papers are specifically indicated in Tables 1 and 2.

ACKNOWLEDGMENTS

The authors thank Anthony M. Carter for providing helpful information and literature, and James R. Stewart, Anthony Carter, Marvalee H. Wake, and Laurie Bonneau for reviewing the manuscript.

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