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REVIEW PAPER DERLEME MAKALESİ

The First and Current Checklist of the Animal Species Bearing Lampbrush Chromosomes

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Abstract: In virtually all animal species, egg cells exhibit a notable size disparity compared to somatic cells in order to support the production of an embryo. The rapid and voluminous production of eggs, often in abundance, necessitates specialized mechanisms. One of these mechanisms is diplotene arrest, a stage characterized by nuclear expansion and heightened chromosomal transcriptional activity, resulting in the formation of distinct lampbrush chromosomes. Lampbrush chromosomes, which are remarkably long, have been best studied in amphibians and birds due to their ease of isolation from the nucleus. A thorough review of scientific literature conducted until March 2025 across electronic databases unveiled the presence of lampbrush chromosomes in a total of 197 animal species, encompassing 31 invertebrates and 166 vertebrates. The widespread occurrence of lampbrush chromosomes across such a diverse array of animal species suggests an ancient evolutionary origin for this mechanism of egg growth.

Keywords: Diploten arrest, egg growth, invertebrates, oogenesis, vertebrates.

Lamba Fırçası Kromozomları Taşıyan Hayvan Türlerinin İlk ve Güncel Listesi

***Sorumlu yazar:**
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Öz: Hemen hemen tüm hayvan türlerinde, yumurta hücreleri embriyo oluşumunu desteklemek amacıyla somatik hücrelere kıyasla belirgin bir boyut farkı gösterir. Yumurtaların hızlı ve bol miktarda üretilmesi genellikle özel mekanizmalar gerektirir. Bu mekanizmalardan biri, çekirdek hacmi ve kromozomlarda transkripsiyon aktivitesi artışı ile karakterize edilen diploten arrestidir; bu süreçte, belirgin lamba fırçası kromozomları ortaya çıkar. Oldukça uzun yapıya sahip olan lamba fırçası kromozomları, çekirdekten izole edilmelerinin kolay olması nedeniyle en iyi amfibilerde ve kuşlarda incelenmiştir. Mart 2025'e kadar elektronik veri tabanları taranarak yapılan kapsamlı bilimsel literatür incelemesi, 31'i omurgasız ve 166'sı omurgalı olmak üzere toplamda 197 hayvan türünde lamba fırçası kromozomlarının varlığını ortaya koymuştur. Bu kromozomların böylesine geniş ve çeşitli hayvan türlerinde görülmesi, yumurta büyümesi için bu mekanizmanın eski bir evrimsel kökene sahip olduğunu düşündürmektedir.

Anahtar kelimeler: Diploten arresti, omurgalılar, omurgasızlar, ovogenez, yumurta büyümesi.

INTRODUCTION

A distinctive feature of the egg cell in all animal species is that it is much larger than the somatic cells of the organism to which it belongs. This size of the egg cell ensures the necessary number of cells for the embryo, stores nutrients that enhance the embryo's survival probability and adaptation success, and makes it easier for the sperm to find the egg, thus increasing the likelihood of fertilization. Animals produce their eggs, which reach large volumes in a short time and can be in large numbers, by using some special mechanisms. One of these mechanisms is diplotene arrest. Developing oocytes enter a waiting stage called diplotene arrest during the prophase of the first meiotic division (prophase I) (Masui, 2001). This waiting stage can last for hours, days, weeks, months, or years depending on the species: in *Clytia hemisphaerica* (Cnidaria, Hydrozoa) it lasts 13-15 hours, in mice it lasts for months, in frogs (*Xenopus*) 2.5-3 years, and in humans, it can last for years (Jessus et al., 2020; Wang and Pepling, 2021). During the diplotene arrest, the nucleus increases in volume, and the chromosomes take on a dense transcriptional activity, forming a characteristic brush-like appearance seen in some vertebrates and invertebrates except mammals, hence termed as lampbrush chromosomes (LBCs). The nucleus in this stage is called the germinal vesicle. The number of nucleoli increases within the germinal vesicle (Coimbra and Azevedo, 1984; Guraya, 1989), excluding adult birds (Koshel et al., 2016), and synthesized histones are stored within it (Jessus et al., 2020).

Brief history: Detailed history of LBCs from their discovery towards mid-1985 can be found in the first chapter of the comprehensive and authoritative book by Professor Harold Garnet Callan (1917-1993). As summarized from this chapter, the history of the discovery and naming of these structures is as follows. LBCs were first observed by the German biologist Walther Flemming (1843-1905), considered the founder of cytogenetics. While studying the egg development of *Siredon pisciformis* (*Ambystoma mexicanum*) with his student, Flemming noticed peculiar, delicate structures in the nuclei of young oocytes in stained preparations. These elongated structures were arranged perpendicular to the long axis and consisted of thin ribbons extending in all directions from the axis. He published these observations in 1882. Flemming later reported similar structures in the nuclei of young oocytes of other salamanders and frogs in his subsequent studies. Carl Rabl (1853–1917), who was an Austrian anatomist, embryologist, and cytologist, observed these structures in the nuclei of *Proteus*, a species of salamander, in 1885, while Moritz Holl (1852-1920), an Austrian anatomist observed them in chicken oocytes in 1890. The German anatomist Johannes Rückert (1854-1923) identified these structures as chromosomes in 1892. During his study on the ovary of *Pristiurus* (*Pristiurus sauteri* or *Pristurus sauteri* valid as *Galeus sauteri*), a shark species, Rückert likened these chromosomes he observed in the nuclei of developing oocytes in sections to brushes used to clean gas lamp glass (similar to brushes used today for cleaning glassware such as test tubes, beakers, and bottles) and named them lampbrush chromosomes (Callan, 1986).

An overview: LBCs are bivalents (tetrads); in each bivalent, two homologous chromosomes (maternal and paternal) are connected at chiasmata points, and thousands of loops extend from the chromatids of each chromosome, one on each side. These loops, due to the accumulation of ribonucleoproteins (RNA polymerases and transcripts), are thicker than the 30 nm thick chromatin fiber, making them easily visible under a light microscope (Sumner, 2003). Loops are sites of intense RNA synthesis. Transcription of genes encoding histones, ribosomal proteins, RNA polymerases, heat shock proteins (hsp70 and hsc90), nuclear lamins, actin, tubulin, calmodulin, metallothionein, DNA polymerase, DNA ligase, enolase, fibronectin, ATP-ADP carrier proteins, nucleophilic proteins N1 and N2, nucleoplasmic proteins, and proteins binding to snRNAs (small nuclear RNAs), as well as genes for ribosomal and transfer RNAs, occurs on loops of various lengths (Macgregor, 1984; Davidson, 1986; Angelier et al., 1996).

LBCs are remarkably long chromosomes; in urodele amphibians such as *Salamandra salamandra* and *Lissotriton vulgaris* (*Triturus vulgaris*), the largest metaphase chromosome adopts a lampbrush form and can reach approximately 700 µm in length. Due to their ease of isolation from the nucleus, LBCs have been best studied in amphibians and birds (Zlotina et al., 2017).

In oogenesis, the duration of chromosomes remaining in the lampbrush form during the diplotene stage varies among species. This duration is a few weeks in *Petromyzon* (Chordata, Petromyzontida), seven months in *Triturus* (Amphibia, Urodela), three months to two years in *Xenopus* frogs (Anura, *Xenopus*), one to one and a half months in *Engystomops* frogs (Anura, *Engystomops*), several months to slightly over a year in lizards (Squamata), three weeks in chickens (*Gallus gallus*), and about three months in grasshoppers (Orthoptera) (Davidson, 1986). For a comprehensive information on both structure and biological role of these gorgeous chromosomes, refer to the review by Saifitdinova et al. (2021), which includes several relevant monographs and a series of review articles.

Cytogenetical significance of LBCs: LBCs have proven to be a crucial tool in cytogenetics due to their unique structural features, with significant applications in cytogenetics, taxonomy, and phylogeny (Macgregor et al., 1990). These features, including lateral loops with unusual morphology, complex organization, associated spherical bodies (Cajal bodies), nucleoli, and distinctive chromomere patterns, serve as marker structures. They allow for the precise identification and mapping of individual chromosomes and specific genome regions, which can be challenging using standard metaphase chromosomes, especially in species with complex karyotypes such as amphibians, birds and reptiles (Dedukh et al., 2013). For example, amphibian chromosomes often lack informative banding patterns, and birds possess small genomes with karyotypes that include a few large macrochromosomes and numerous indistinguishable microchromosomes (Zlotina et al., 2017). As a result, traditional cytogenetic methods, particularly those relying on compact metaphase chromosomes, are often inadequate for studying the karyotypes of these animals.

Moreover, LBC analysis enables the construction of comprehensive cytological maps, providing a high-resolution framework for fluorescence in situ hybridization (FISH) mapping of genomic fragments. This makes LBCs a powerful tool for high-resolution karyotype analysis. In addition, inter- and intrachromosomal rearrangements such as inversions, fusions, and translocations can be detected through the analysis of orthologous LBCs (Dedukh et al., 2013; Zlotina et al., 2017). In bird and reptile species with complex karyotypes, especially those enriched with repetitive elements, LBC analysis helps reveal the order of cytological markers, shedding light on chromosomal evolution, including the differentiation of sex chromosomes (Keinath et al., 2021). It should be also noted that LBCs are a unique model object for the cyto-molecular analysis of transcription and co-transcriptional processing of synthesized RNA (Saifitdinova et al., 2021).

LBCs are not only valuable for mapping individual chromosomes but also for studying evolutionary relationships between species. The positions and distribution of various landmark loops on LBCs often correlate with phylogenetic relationships, with closely related species exhibiting similar landmark patterns. This has enabled researchers to explore phylogenetic connections among species such as urodeles and anurans. However, the analysis of more distantly related species remains challenging with this method (Macgregor et al., 1990; Ohtani, 1990; Zlotina et al., 2017).

In addition to interspecies analysis, LBCs can be used to investigate intraspecies genetic polymorphisms. Variability in the landmark structures of LBCs in animals from isolated populations suggests the accumulation of polymorphisms, which is a key factor in the early stages of allopatric speciation. Furthermore, the analysis of chiasmata distribution on LBCs aids in identifying sex chromosomes, particularly when they are indistinguishable at metaphase (Bucci et al., 1990; Zlotina et al., 2017).

The application of LBCs extends to high-resolution physical gene mapping, allowing for the precise localization of individual genes or tandem repeat families on specific chromomeres or lateral loops. FISH techniques can be employed to map these genetic elements, providing insights into the patterns of DNA/DNA and DNA/RNA hybridization. Additionally, LBCs facilitate the investigation of epigenetic modifications within both decondensed (lateral loops) and condensed (chromomeres) chromatin domains, further enhancing their value in cytogenetic research (Kulikova et al., 2020).

In conclusion, LBCs represent an invaluable tool for cytogenetic and cytological studies, offering high-resolution insights into genome structure, chromosomal evolution, and species relationships. Their applications span various fields, from taxonomy and phylogeny to the study of genetic polymorphisms and chromosomal rearrangements.

Checklist: As of the beginning of March 2025, animal species in which LBCs have been detected in their oocytes during oogenesis are listed in Tables 1 and 2, following the completion of a comprehensive literature search through electronic databases for pertinent scientific articles. As can be seen from the accompanying tables, a total of 197 animal species, comprising 31 invertebrates (Table 1) and 166 vertebrates (Table 2), possess these chromosomes. The earliest articles reporting lampbrush chromosome studies in the relevant animal species have been cited in the tables, excluding more recent ones reporting the same species. Additionally, the taxon names mentioned in the cited articles have been used. The tables are annually updated by us and can be accessed through the page http://spass-sci.ru/lbc/supplementary.htm, originally launched by the late Professor Herbert Macgregor (1933–2018), currently maintained by the Saint Petersburg Lampbrushology Scientific School (Russia) and are available to the general public.

Table 1. The invertebrate species in which LBCs have been reported from their oocytes during oogenesis.

Taxa	Species	References*
Cnidaria: Anthozoa	*Nematostella vectensis*	Moiseeva et al., 2017
Crustacea: Isopoda	*Anilocra physodes*	Callan, 1957
Crustacea: Decapoda	*Macrobrachium amazonicum*	Paschoal and Zara, 2023
Insecta: Diptera	*Calliphora erythrocephala*	Dävring, 1983
	Drosophila melanogaster *Drosophila hydei* *Drosophila funebris*	Dävring and Sunner, 1982
Insecta: Orthoptera	*Locusta migratoria*	Kunz, 1967a
	Homorocoryphus nitidulus *Acrida bicolor* *Decticus albifrons*	Kunz, 1967b
	Gryllus domesticus (*Acheta domesticus*)	Kunz, 1969
Insecta: Dictyoptera	*Blattella germanica*	Bier et al., 1967
Insecta: Coleoptera	*Carabus granulatus* *Carabus nemoralis* *Pterostichus vulgaris* *Pterostichus niger* *Abax ater*	Bier et al., 1967; Callan, 1986
Insecta: Hymenoptera	*Diplolepis rosae*	Stille and Dävring, 1980
Insecta: Lepidoptera	*Ephestia kuehniella*	Weith and Traut, 1980
Insecta: Zygentoma	*Thermobia domestica*	Tworzydlo et al., 2017
Arachnida: Trombidiformes	*Trombidium latum*	Derdak et al., 2024
Mollusca: Gastropoda	*Bithynia tentaculata*	Bottke, 1973
Mollusca: Cephalopoda	*Sepia officinalis*	Callan, 1957
Chaetognatha: Sagittoidea	*Ferosagitta ferox* *Flaccisagitta hexaptera* *Sagitta bipunctata* *Sagitta elegans* *Sagitta maxima* *Sagitta pulchra*	Mishin, 1980
Echinodermata: Asteroidea	*Echinaster sepositus*	Delobel & Delavault, 1971

* Although there is more than one related article, the earliest one was included.

CONCLUSION

The almost universal presence of LBCs in such a diverse range of animal species suggests that this mechanism of egg growth likely has a very ancient evolutionary origin. This checklist, the first of its kind, aims to serve as a valuable database for researchers new to the study of LBCs, providing information on their occurrence in nature along with essential introductory details about these fascinating and evolutionarily significant chromosomes.

Table 2. The vertebrate species in which LBCs have been reported from their oocytes during oogenesis.

Taxa	Species	References**
Cyclostomata	*Petromyzon marinus**	Davidson, 1986
Pisces: Chondrichthyes	*Scyllium catulus*	Callan, 1957
	*Pristiurus melanostomus** *Squalus suckleyi** *Torpedo**	Callan, 1986
	Callorhinchus callorynchus	Fuentes et al., 2023
	Scyliorhinus canicula	Porceddu et al., 2024
Pisces: Osteichthyes	*Brachydanio rerio*	Baumeister, 1973
	*Gasterosteus aculeatus** *Trigla hirundo**	Callan, 1986
	Heterandria formosa	Uribe and Grier, 2011
	Cyprinodon variegatus	Wallace & Selman, 1981
	Scomber scomber	Bara, 1960
	Micropterus salmoides	Żelazowska & Halajian, 2019
	Labeobarbus marequensis	Żelazowska & Halajian, 2020
	Cobitis elongatoides *Cobitis taenia*	Marta et al., 2020
	Sander lucioperca	Żelazowska & Kujawa, 2022
	Mullus surmuletus	Berthelin et al., 2022
	Poecilia mexicana *Poecilia formosa*	Dedukh et al., 2022
	Acipenser ruthenus	Iegorova et al., 2022
	Pleuronectes platessa	Sauger et al., 2023
	Cyprinodon artifrons *Garmanella pulchra*	Omar, 2024
	Cobitis hankugensis *Iksookimia longicorpa*	Dedukh et al., 2024a
	Gymnocorymbus ternetzi	Domínguez-Castanedo et al., 2024
	Lepidorhombus whiffiagonis	Kellner et al., 2024a
	Lepidorhombus boscii	Kellner et al., 2024b
	Silonia silondia	Akhi et al., 2024
	Hybrids between *Clarias macrocephalus* and *Clarias gariepinus*	Dedukh et al., 2024b
	Danio rerio	Dedukh et al., 2025
Amphibia: Urodela	*Ambystoma jeffersonianum* *Ambystoma laterale*	Macgregor & Uzzell, 1964; Bi & Bogart, 2010
	Ambystoma macrodactylum *Ambystoma gracile* *Ambystoma tremblayi*	Kezer et al., 1980
	Ambystoma mexicanum	Callan, 1966
	Ambystoma tigrinum	Gall, 1954
	Ambystoma texanum	Bogart, 2003
	*Amphiuma means**	Callan, 1986
	Bolitoglossa subpalmata	Macgregor, 1980
	*Euproctus montanus** *Euproctus platycephalus**	Nardi et al., 1972
	Hynobius quelpaertensis	Ikebe et al., 2005
	Necturus maculatus (*maculosus*) *Pseudotriton montanus*	Lafontaine & Ris, 1958

Table 2. (Continued)

Taxa	Species	References**
Amphibia: Urodela	*Plethodon cinereus cinereus* *Plethodon cinereus polycentratus* *Plethodon nettingi hubrichti* *Plethodon richmondi* *Plethodon dorsalis* *Plethodon dunni* *Plethodon vehiculum* *Eurycea bislineata bislineata* *Eurycea lucifuga*	Kezer & Macgregor, 1973
	Pleurodeles poireti *Pleurodeles waltlii* (*waltl*)	Lacroix, 1968
	*Proteus anguineus**	Callan, 1986
	Salamandra salamandra	Mancino et al., 1969
	Siren intermedia	Leon and Kezer, 1974
	Taricha granulosa	Fabergé, 1970
	*Taricha torosa**	Callan, 1986
	Notophthalmus (*Triturus*) *viridescens*	Gall, 1954
	Triturus carnifex *Triturus cristatus* *Triturus dobrogicus* (*danubialis*) *Triturus karelinii*	Callan & Lloyd, 1960
	Triturus helveticus	Mancino & Barsacchi, 1966
	Triturus italicus	Mancino & Barsacchi, 1969
	Triturus vulgaris meridionalis	Barsacchi et al., 1970
	Triturus alpestris apuanus	Ragghianti et al., 1972
	Triturus marmoratus	Nardi et al., 1972
	Triturus montandoni	Ragghianti et al., 1978
	Triturus boscai *Triturus vittatus ophryticus*	Bucci-Innocenti et al., 1983
	Cynops (*Triturus*) *pyrrhogaster*	Imoh, 1981
Amphibia: Anura	*Ascaphus truei*	Macgregor & Kezer, 1970
	Bombina variegata *Bufo bufo* *Bufo calamita* *Bufo viridis*	Ullerich, 1970
	Bufo lentiginosus	King, 1908
	Flectonotus pygmaeus	Macgregor & del Pino, 1982
	Agalychnis callidryas *Bufo marinus* *Bufo typhonius* *Colostethus inguinalis* *Dendrobates auratus* *Engystomops pustulosus* *Hyla ebraccata* *Hyla rosenbergi* *Leptodactylus pentadactylus*	Davidson & Hough, 1969
	Pelophylax (*Rana*) *lessonae* *Pelophylax* (*Rana*) *ridibundus*	Dedukh et al., 2013

Table 2. (Continued)

Taxa	**Species**	**References****
Amphibia: Anura	*Rana catesbeiana* (*Lithobates catesbeianus*)	Wu et al., 1986
	Rana (*Euphlyctis*) *cyanophlyctis*	Srivastava & Bhatnagar, 1962
	Rana epeirotica *Rana shqiperica*	Guerrini et al., 1997
	Rana esculenta	Giorgi & Galleni, 1972
	*Rana fusca**	Callan, 1986
	Rana pipiens	Rogers & Browder, 1977
	Rana temporaria	Tsvetkov & Parfenov, 1994
	Rana nigromaculata *Rana brevipoda* *Rana plancyi chosenia* *Rana plancyi fukienensis*	Ohtani, 1990
	Rana porosa	Ohtani, 1995
	Rana rugosa	Miura et al., 1996
	Xenopus laevis	Müller, 1974
	Xenopus tropicalis	Penrad-Mobayed et al., 2009
	Rhinella schneideri	Montezol et al., 2018
	Pelophylax perezi	Dudzik et al., 2023
Reptilia	*Hoplodactylus maculatus* (*Woodworthia maculatus*)	Boyd, 1940
	Platydactylus muralis (*Platydactylus fascicularis*, *Tarentola mauritanica*)* *Anguis fragilis** *Testudo hermani** *Crocodylus niloticus** *Lacerta muralis** *Lacerta stirpium** *Lacerta viridis** *Lacerta vivipara** *Uromastix achantinurus**	Callan, 1986
	Lacerta armeniaca *Lacerta rostombekovi* *Lacerta dahli* *Lacerta saxicola* (*L. s. defilippii, L. s. portschinskii, L. s. valentini*) *Eremias velox* *Eremias strauchi* *Ophisops elegans* *Agama caucasica* *Phrynocephalus helioscopus* *Phrynocephalus reticulatus*	Arronet, 1973
	Bipes biporus *Bipes canaliculatus*	Macgregor & Klosterman, 1979
	*Cistudo europaea** *Pseudemys scripta elegans*	Callebaut et al., 1997
	Darevskia armeniaca *Lacerta agilis* *Podarcis tauricus* *Zootoca vivipara*	Lukina, 1994

Table 2. (Continued)

Taxa	Species	References**
Reptilia	*Pelodiseus sinensis*	Hei et al., 2010
	Trachemys scripta	Davidian et al., 2021
	Chalcides ocellatus	Ibrahim & Wilson, 1989
	Sceloporus torquatus torquatus	Uribe et al., 1995
	Mabuya brachypoda	Hernández-Franyutti et al., 2005
	Hemidactylus flaviviridis	Al-Amri, 2012
	Salvator merianae	García-Valdez et al., 2019
	Alligator mississippiensis	Uribe & Guillette, 2000
	Caiman latirostris	Machado-Santos et al., 2015
	Zootoca vivipara	Kupriyanova & Safronova, 2023
	Alligator sinensis	Nie et al., 2023
Aves	*Apus apus*	Gaginskaya, 1972; Solovei et al., 1993
	Fringilla montifringilla	
	Caprodaca erythrinus	
	Spinus spinus	
	Anthus trivialis	
	Turdus iliacus	
	Gallus gallus domesticus	
	Coturnix coturnix japonica	
	Meleagris gallopavo	
	Columba livia	
	Passer domesticus	
	Fringilla coelebs	
	Taeniopygia guttata	Torgasheva et al., 2019

* The articles of these species could not be found, but they were attributed in the relevant cited reference.
** Although there is more than one related article, the earliest one was included.

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