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PHYLOGENY AND CLASSIFICATION OF LEPORIDAE (MAMMALIA, LAGOMORPHA)

A. O. Averianov

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg, 199034, Russia.

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Phylogeny and Classification of Leporidae (Mammalia, Lagomorpha). Averianov A. O. — New phylogenetic analysis of 28 genera of Neogene-Recent Leporidae based on 30 morphological characters is provided. Five new suprageneric taxa are established: Neolagomorpha, suborder n., Ochotonida, order-group taxon n., Leporida, order-group taxon n., Notolagini, triba n., Bunolagini, triba n.

Key words: Logonorpha, Leporidae, phylogeny, classification.

Филогения и классификация Leporidae (Mammalia, Lagomorpha). Аверьянов А. О. — Проведен новый филогенетический анализ 28 родов неоген-современных Leporidae, основанный на 30 морфологических признаках. Установлено 5 надродовых групп: Neolagomorpha, suborder n., Ochotonida, order-group taxon n., Leporida, order-group taxon n., Notolagini, triba n., Bunolagini, triba n.

Ключевые слова: Logonorpha, Leporidae, филогения, классификация.

Introduction

The first reliable suprageneric classification of Leporidae, based on p3 morphology solely, was done by Dice (1929). He divided family into 3 subfamilies: Palaeolaginae (p3 with both PIR and PER), Archaeolaginae (p3 without PIR, PER crossing no more than half of the p3 occlusal surface), and Leporinae (p3 with only PER, crossing nearly to the lingual side of the tooth). An attempt to make a cladistic analysis of Leporidae was done by Angermann (1974), but results were not published. Some morphological characters for Leporidae were scored by Corbet (1983) without an attempt to analyse data. Preliminary phylogenetic analysis of selected leporid genera was made by McKenna (1982) and Averianov (1994a). Here a new analysis included all known Neogene-Recent leporid genera (excluding *Panolax* Cope, 1874, nomen dubium) and based on all available diagnostic characters is provided.

Dental terminology is after White (1987).

Abbreviations: AER — anteroexternal reentrant (Fig. 1); AIR — anterointernal reentrant; AR — anterior reentrant; PER — posteroexternal reentrant; PIR — posterointernal reentrant. Capital and lower case letters: I/i (incisor), P/p (premolar) and M/m (molar), refer to upper and lower teeth. Asterisk after a character (*) denotes parallelism, "R" — reversal.

Characters

1. Postorbital processes weakly developed, without an anterior projection (0); better developed, with both anterior and posterior projections (1).

2. Interparietal fused with parietals in adults (0); separated in adults (1).

3. Maximal width of incisive foramen is less then the length of bone palate (0); exceed the length of bone palate (1).

4. Relative length of the bone palate, as percentage of condilobasal skull length: >14% (0); 10–14% (1); <10% (2).

5. Relative width of the choanae ("mesopterygoid fossa"), as percentage of condilobasal skull length: =10% (0); >10% (1).

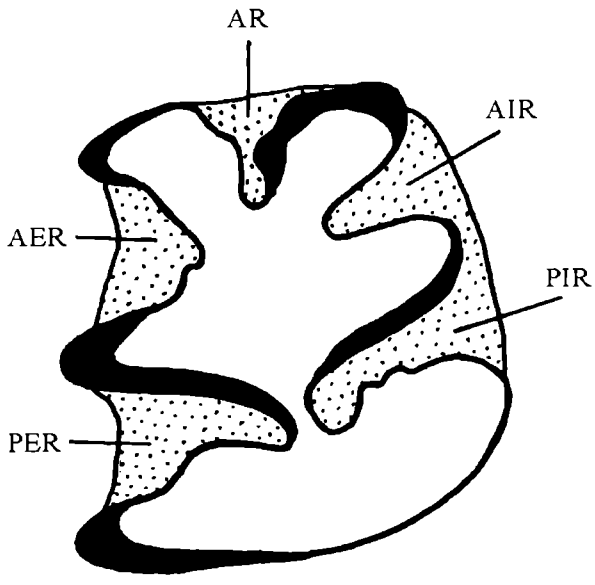

Fig. 1. Diagram of the occlusal surface of left leporid p3 showing main reentrants (from White, 1987).

Рис. 1. Схема жевательной поверхности левого p3 зайцеобразных, демонстрирующая основные вхождения (по White, 1987).

6. Auditory bullae small, in length less then the occipital condyle (0); middle sized, approximately equal in length to the occipital condyle (1); very large, exceeds by 1.5 or more times the length of the occipital condyle (2).

7. Notch on anterior surface of I2 shallow, simple, lacking cement (0); more deep, simple, filled by cement (1); deep and divided into 2–3 branches or there are 2–3 notches filled by cement (2).

8. P3–4 less molariform than M1–2, with crescent on unworn teeth (0); completely molariform (1).

9. P2 with 1 anterior reentrant (0); with 2 reentrants (1); with 3 and more reentrants (3).

10. Hypostria on P3-M2 shallow, less than half of the crown width, with straight walls (0); more deep, more than half of the crown width, with slightly crenulated walls (1); deep, with strongly crenulated walls (3).

11. M3 is relatively unreduced, its width =40% of the width of M2 (0); more reduced, width <40% of the width of M2 (1); absent at least in the majority of population (2).

12. i2 begins at m2 (0); at p4-m1 (1); at p3 (2); anterior to p3 (3).

13. p3 without an AR (0); with 1 AR (1); with 2 or more AR (2).

14. AER on p3 shallow, lacking cement (0); more deep, filled by cement (1).

15. p3 without an AIR or this reentrant shallow, lacking cement (0); AIR shallow, but filled by cement (1); AIR more deep, longer than PIR or equal to AER (2); AIR very deep, equal approximately to half of the crown length (3).

16. On p3 AIR and/or AER with straight walls (0); with crenulated walls (1).

17. Posterior reentrants on p3: there is only PER, crossing no more than half of the occlusal surface (0); there are both PER and PIR (1); there are open PER and PIR closed into an enamel lake (2); PER and PIR fused, forming long hypoflexid crossing nearly to the lingual side of the tooth (3).

18. Posterior walls of PIR and/or PER on p3 straight (0); slightly crenulated (1); strongly crenulated (2).

19. Anterior wall of talonid on p4-m2 straight (0); slightly crenulated (1); strongly crenulated (2).

20. Relative length of neural spines in anterior thoracic vertebrae: short, no longer than 2.5 times of the vertebra centrum length (0); longer, between 2.5–3 times of the vertebra centrum length (1); long, more than 3 times of the vertebra centrum length (2).

21. Transverse processes of the sacral vertebrae broad and long (0); of moderate width, long (1); narrow and very long (2).

22. Number of caudal vertebrae: =10 (0); <10 (1).

23. Lateral processes of presternum large and broad (0); weak (1); nearly absent (2).

24. Ventral part in anterior ribs narrow (0); widened (1).

25. Ulna (without olecranon) in length less then or equal to humerus (0); exceed the length of humerus (1).

26. Length of hind feet, as percentage of condylobasal skull length: 80–120% (0); >120% (1).

27. Texture of pelage: normal (0); soft (1); harsh (2).

28. Ventral pelage: uniformly brown (agouti) (0); pale with grey bases and underfur (1).

29. Pectoral mane of the same colour as the ventral pelage (0); sharply contrasts in colour with white ventral pelage (1).

30. Diploid number of chromosomes, 2n: =48 (0); 46 (1); 44 (2); 42 (3); 38 (4).

31. Geographical centre of origin for the genus: North America (0); Eurasia (1); Africa (2). This implies that genera originated on one continent may be more closely related to each other than to genera from other continents and reflects dispersal of the family from North America to Africa through Eurasia.

Phylogenetic analysis

Taxon-character matrix (table 1) plotted 28 genera and 31 characters. *Archaeolagus* was used as the outgroup. Multistate characters were coded as additive (ordered). Differential weighting was applied *a priori* (weigh 5 for character 15, weight 10 for char-

Table 1. Taxon-character matrix for 28 leporid genera

Таблица 1. Матрица таксономических признаков для 28 родов зайцеобразных

Taxa	Characters
Archaeolagus	0 0 0 ? ? 1 0 0 0 0 0 1 0 0 0 0 0 0 0 ? 1 ? ? 1 0 ? ? ? ? ? 0
Hypolagus	0 1 1 2 1 1 0 1 0 1 0 2 0 1 0 0 0 0 0 ? ? ? ? ? ? 0 ? ? ? ? ? 0
Pewelagus	1 1 1 2 0 2 0 1 0 1 0 2 0 1 0 1 0 1 1 ? ? ? ? ? ? ? ? ? ? ? 0
Lepoides	? ? ? ? ? ? 0 1 2 1 ? 2 1 1 0 0 0 0 1 ? ? ? ? ? ? ? ? ? ? ? 0
Alilepus	0 0 1 2 1 0 0 1 0 1 1 3 0 1 0 0 1 0 0 ? ? ? ? ? 0 ? ? ? ? ? 0
Pronotolagus	? ? ? ? ? ? ? 1 ? 1 ? 2 0 1 2 0 1 0 0 ? ? ? ? ? ? ? ? ? ? ? 0
Notolagus	? ? 1 ? ? ? 1 1 2 1 1 2 0 1 3 1 1 1 0 ? ? ? ? ? ? ? ? ? ? ? 0
Paranotolagus	? ? ? ? ? ? 2 1 ? 2 ? 2 1 1 3 1 1 2 2 ? ? ? ? ? ? ? ? ? ? ? 0
Pliopentalagus	? ? ? 0 ? ? 0 1 2 1 ? 2 2 1 1 0 1 2 1 ? ? ? ? ? ? ? ? ? ? ? 1
Pentalagus	0 0 0 0 0 0 0 1 2 2 2 2 2 1 1 0 1 2 2 1 0 0 0 0 0 0 0 0 0 1 1
Sericolagus	? ? ? ? ? ? ? ? ? ? ? 1 0 1 0 0 1 0 1 ? 0 ? ? ? ? ? ? ? ? ? 1
Trischizolagus	1 ? 1 ? ? ? 0 1 2 1 1 2 1 1 1 0 1 0 0 ? ? ? ? ? ? ? ? ? ? ? 1
Serengetilagus	1 1 1 2 1 ? 1 1 1 1 1 2 2 1 1 0 1 0 0 ? ? ? ? ? 0 ? ? ? ? ? 2
Pronolagus	1 0 1 1 0 0 0 1 1 1 0 3 1 1 1 0 1 0 0 1 2 0 1 0 0 0 1 1 1 3 2
Bunolagus	1 1 1 1 1 1 0 1 0 1 0 ? 1 1 0 0 1 0 0 ? ? 0 ? ? ? 1 1 1 1 2 2
Aztlanolagus	? ? 0 ? ? ? ? 1 2 1 1 3 1 1 1 0 2 2 2 ? ? ? ? ? ? ? ? ? ? ? 0
Pratilepus	? ? ? ? ? ? ? 1 2 1 ? ? 0 1 1 1 2 2 2 ? ? ? ? ? ? ? ? ? ? ? 0
Nekrolagus	0 ? 1 2 0 1 ? 1 2 1 0 ? 1 1 0 0 2 1 0 ? ? ? ? ? ? ? ? ? ? ? 0
Romerolagus	0 1 0 1 0 1 0 1 2 1 1 2 0 1 0 0 2 1 1 0 1 1 0 0 0 0 0 0 0 0 0
Aluralagus	? ? 1 ? ? ? ? 1 2 1 0 2 0 1 0 1 3 2 2 ? ? ? ? ? ? ? ? ? ? ? 0
Brachylagus	1 1 1 2 0 2 0 1 0 1 1 2 0 1 0 0 3 0 0 1 2 1 2 0 0 1 1 1 1 2 0
Sylvilagus	1 1 1 1 1 1 1 1 2 1 0 2 2 1 0 1 3 1 1 1 2 0 2 0 0 1 1 1 1 4 0
Nesolagus	0 0 0 0 0 0 0 1 0 0 0 2 0 1 0 0 3 0 0 ? 1 1 0 0 0 0 0 1 1 ? 1
Caprolagus	0 0 0 1 0 0 1 1 2 1 1 1 2 1 2 0 3 1 2 1 1 1 0 0 0 0 2 1 1 ? 1
Poelagus	0 0 1 1 0 1 1 1 2 1 1 2 1 1 2 1 3 1 1 ? 2 0 ? 0 0 1 0 1 1 ? 2
Oryctolagus	1 1 1 2 0 1 0 1 2 1 1 2 1 1 0 0 3 0 0 2 2 0 0 0 0 1 1 1 1 2 1
Indolagus	1 0 1 1 0 1 2 1 2 1 0 2 1 1 0 1 3 1 1 ? 2 0 2 1 1 1 0 1 1 ? 1
Lepus	1 0 1 2 1 1 0 1 2 1 1 3 1 1 0 0 3 0 0 2 2 0 2 1 1 1 1 1 1 0 1

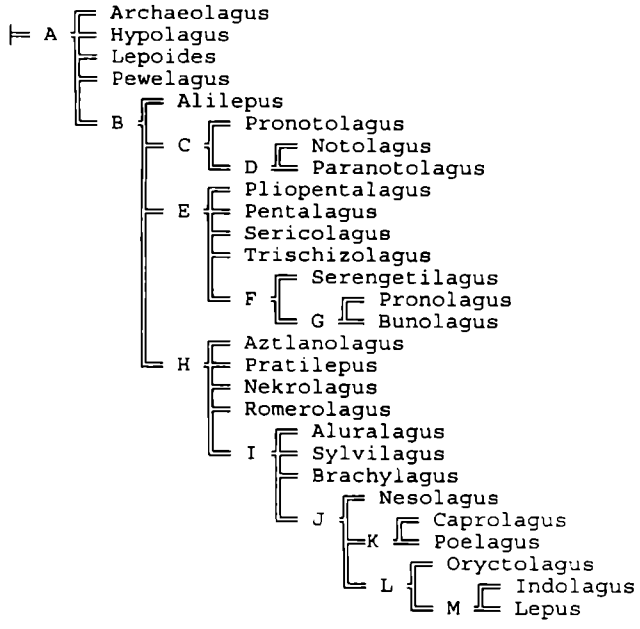

Fig. 2. Hypothesis of the phylogenetic relationships among the known leporid genera.

Рис. 2. Гипотеза о филогенетических связях между известными родами зайцеобразных.

acter 17, weight 20 for character 31, and weight 1 for the remaining characters) and *a posteriori* (successive weighting). The *a priori* weighting of fully determinate characters was applied to help reduce problems of homoplasy. An equal weights or solely successive weighting analysis of this data set generated the cladogram representing the mixture of combined together Old World and New World taxa, which seems to be not natural. Resulting, the analysis performing an *a priori* and successive weighting have been chosen as producing the best estimation of leporid phylogeny.

The matrix was run by HENNIG 86 computer program using mhennig* and bb* algorithms. The successive weighting required four steps (trees/length/ci/ri = 16/302/0.43/0.77; 3276(overflow)/150/0.65/0.83; 3276(overflow)/140/0.75/0.90; 3276(overflow)/147/0.72/0.89). The nelsen (strict) consensus tree for the last analysis is represented on Fig. 2. It has length 160 steps, ci=0.66, ri=0.86.

Phylogeny

In the classification presented here the node-based definition of taxa (de Queiroz, Gauthier, 1990) and the metataxon concept (Archibald, 1994) were used. Paraphyletic taxa are in quotation marks.

Order Lagomorpha Brandt, 1855

Definition: all Duplicidentata Illiger, 1811 except "Mimotonida" (order-group ambitaxon, genera listed in Averianov, 1994b and McKenna & Bell, 1997). For the "stem-modified node-based definition" of Lagomorpha see Wyss & Meng, 1996.

Diagnosis: tooth germs of p2 and p3 fused; i3 lost; diastema between i2 and p3 increased; I2 with groove on anterior surface.

Neolagomorpha, suborder n.

Definition: the most recent common ancestor of *Lepus* Linnaeus, *Ochotona* Link, 1795, and *Palaeolagus* Leidy, 1856, and all of its descendants.

Diagnosis: bone palate terminates within tooth row; cheek teeth with cement; P4 molariform; P3, 4 and M1, 2 with hypostriae; M2, 3 without postcingulum; M3 reduced; i2 begins at p4 or more anteriorly.

"Palaeolagida" Haeckel, 1895, **order-group ambitaxon**

Definition: all Neolagomorpha except Ochotonida and Leporida, as defined below.

Ochotonida, order-group taxon n.

Definition: the most recent common ancestor of Ochotonidae Thomas, 1897 and "Amphilagidae" Gureev, 1953 (ambitaxon) (genera listed in Erbaeva, 1988), and all of its descendants.

Diagnosis: M3 lost.

Clade A: Leporida, order-group taxon n.

Definition: the most recent common ancestor of Leporoidea as defined below, *Litolagus* Dawson, 1958, and *Archaeolagus* Dice, 1917, and all of its descendants.

Diagnosis: 2(1), 3(1), 4(2), 8(1), 10(1), 12(2), 14(1), 20(1), 21(1).

Clade B: Family Leporidae Fischer, 1817

Definition: crown-group, the most recent common ancestor of *Pentalagus* Lyon, 1904 and *Lepus* Linnaeus, 1758, and all of its descendants.

Diagnosis: 9(2), 11(1), 17(1).

Comment: characters 27(1), 28(1), 29(1) may be diagnostic at this node (ACCTRAN optimisation, implies reversals 27(0) in *Romerolagus*, *Pentalagus*, *Nesolagus*, *Poelagus*, and *Indolagus*; 28(0) and 29(0) in *Romerolagus* and *Pentalagus*). The alternative interpretation (DELTRAN optimisation) implies parallel development of these characters at nodes G and I.

Clade C: Tribe Notolagini, triba n.

Definition: the most recent common ancestor of *Notolagus* Wilson, 1938, *Paranotolagus* Miller & Carranza-Castañeda, 1982, *Pronotolagus* White, 1991, and all of its descendants.

Type genus: *Notolagus* Wilson, 1938.

Diagnosis: 15(2)*.

Clade D: unnamed family-group taxon

Diagnosis: 7(1)*, 15(3), 16(1), 18(1)*.

Clade E. Subfamily Pentalaginae Gureev, 1948

Definition: the most recent common ancestor of *Pentalagus* Lyon, 1904 and *Bunolagus* Thomas, 1929, and all of its descendants.

Diagnosis: 13(1), 15(1).

Comment: Radiation of the pentalagines followed one dispersal event, penetrating of a North American species of *Alilepus* into Eurasia via Beringida [31(1)] during the middle Miocene thermal optimum (early Vallesian). So designated here the *Alilepus* dispersal event was approximately contemporaneous with the *Hipparion* dispersal event (ca. 11 Ma).

Clade F: Tribe Bunolagini, triba n.

Definition: the most recent common ancestor of *Bunolagus* Thomas, 1929 and *Serengetilagus* Dietrich, 1941, and all of its descendants.

Type genus: *Bunolagus* Thomas, 1929.

Diagnosis: 1(1)*, 4(1)*, 9(1).

Comment: Radiation of Bunolagini followed one dispersal event, penetrating of *Alilepus*-like ancestral form into Africa from Eurasia [31(2)] during the late Miocene (ca. 6 Ma).

Clade G: unnamed family-group taxon

Diagnosis: 11(0)R.

Clade H: Subfamily Leporinae Fischer, 1817

Definition: the most recent common ancestor of *Romerolagus* Merriam, 1896 and *Lepus* Linnaeus, 1758, and all of its descendants.

Diagnosis: 13(0)R, 17(2), 18(1)*, 19(1).

Clade I: unnamed family-group taxon

Diagnosis: 17(3), 21(2), 26(1).

Clade J: unnamed family-group taxon

Diagnosis: 2(0)R, 13(1).

Comment: Our phylogeny implies the second dispersal event: penetration of an leporine from North America to Eurasia followed by the radiation of the clade J. Currently this event cannot be traced in the fossil record.

Clade K: unnamed family-group taxon

Diagnosis: 4(1)*, 7(1)*, 15(2)*.

Clade L: Tribe Oryctolagini Gureev, 1948

Definition: the most recent common ancestor of *Oryctolagus* Lilljeborg, 1874 and *Lepus* Linnaeus, 1758, and all of its descendants.

Diagnosis: 1(1)*, 20(2).

Clade M: Subtribe Leporini Fischer, 1817

Definition: the most recent common ancestor of *Indolagus* Gureev, 1964 and *Lepus* Linnaeus, 1758, and all of its descendants.

Diagnosis: 23(2), 24(1), 25(1).

Classification

The phylogenetic classification of leporids appears as the following:

Order Lagomorpha Brandt, 1855
Suborder Neolagomorpha, suborder n.
†"Palaeolagida" Haeckel, 1895, paraphyletic order-group ambitaxon
Ochotonida, order-group taxon n.
Leporida, order-group taxon n.
†*Litolagus* Dawson, 1958
†Subfamily "Archaeolaginae" Dice, 1929, paraphyletic stem-group mixotaxon
†*Archaeolagus* Dice, 1917
†*Hypolagus* Dice, 1917
†*Pewelagus* White, 1984
†*Lepoides* White, 1987
Family Leporidae Fischer, 1817
†*Alilepus* Dice, 1931
†Tribe Notolagini, triba n.
†*Pronotolagus* White, 1991
†*Notolagus* Wilson, 1938
†*Paranotolagus* Miller & Carranza-Castañeda, 1982
Subfamily Pentalaginae Gureev, 1948
†*Pliopentalagus* Gureev & Konkova, 1964
Pentalagus Lyon, 1904
†*Sericolagus* Averianov, 1996
†*Trischizolagus* Radulesco & Samson, 1967
Tribe Bunolagini, triba n.
†*Serengetilagus* Dietrich, 1941
Pronolagus Lyon, 1904
Bunolagus Thomas, 1929
Subfamily Leporinae Fischer, 1817
†*Aztlanolagus* Russell & Harris, 1986
†*Pratilepus* Hibbard, 1939
†*Nekrolagus* Hibbard, 1939
Romerolagus Merriam, 1896
unnamed family-group taxon. Leporines with "*Lepus*"-like p3.
†*Aluralagus* Downey, 1968
Brachylagus Miller, 1900
Sylvilagus Gray, 1867
unnamed family-group taxon. Old World leporines.
Nesolagus Forsyth Major, 1899
Caprolagus Blyth, 1845
Poelagus St. Leger, 1932
Tribe Oryctolagini Gureev, 1948
Oryctolagus Lilljeborg, 1874
Subtribe Leporini Fischer, 1817
Indolagus Gureev, 1964
Lepus Linnaeus, 1758

Ангерманн Р. Распространение и аспекты родственных отношений современных представителей семейства Leporidae (Lagomorpha) // I Междунар. териол. конгр. : Реф. докл. — М., 1974. — Т. 1. — С. 28–29.

Аверьянов А. О. О положении рода Lepus в системе семейства Leporidae (Mammalia, Lagomorpha) // Зоол. журн. — 1994а. — **73**, вып. 10. — С. 97–107.

Ербаева М. А. Пищухи Кайнозоя (таксономия, систематика, филогения). — М. : Наука, 1988. — 222 с.

Averianov A. O. Early Eocene mimotonids of Kyrgyzstan and the problem of Mixodontia // Acta Palaeontol. Polon. — 1994b. — **39**, № 4. — P. 393–411.

Archibald J. D. Metataxon concepts and assessing possible ancestry using phylogenetic systematics // Syst. Biol. — 1994. — **43**. № 1. — P. 27–40.

Corbet G. B. A review of classification of the family Leporidae // Acta Zool. Fennica. — 1983. — № 174. — P. 11–15.

Queiroz de K., Gauthier J. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names // Syst. Biol. — 1990. — **39**, № 4. — P. 307–322.

Dice L. R. The phylogeny of the Leporidae, with description of a new genus // J. Mammal. — 1929. — **10**, № 4. — P. 340–344.

McKenna M. Lagomorph interrelationships // Geobios, Mem. spec. — 1982. — № 6. — P. 213–223.

McKenna M. C., Bell S. K. Classification of mammals above the species level. — New York : Columbia Univ. Press, 1997. — 631 p.

White J. A. The Archeolaginae (Mammalia: Lagomorpha) of North America, excluding Archaeolagus and Panolax // J. Verteb. Paleontol. — 1987. — **7**, № 4. — P. 425–450.

Wyss A. R., Meng J. Application of phylogenetic taxonomy to poorly resolved crown clades: a stem-modified node-based definition of Rodentia // Syst. Biol. — 1996. — **45**, № 4. — P. 559–568.