Estimations of global extant spider family richness using neontological and palaeontological data

Оценки глоального богатства семейств пауков исходя из неонтологичеких и палеонтологических данных

D. PENNEY

Department of Earth Sciences, The University of Manchester, Oxford Road, Manchester, M13 9PL, United Kingdom. email: david.penney@man.ac.uk

ABSTRACT. Given the present rate of global change and species extinctions, the task of assessing global biodiversity requires that we estimate and extrapolate biological inventory data. Global spider family richness is estimated with existing extrapolative techniques in a novel manner, using data based on the number of described spider families over time in years, which are considered as incremental knowledge units. A novel technique combining palaeontological and neontological data is employed to obtain another, independent estimate. Lower bound estimates of global spider family richness from the existing techniques range from 110–112. An upper bound estimate from the new technique is 124. The actual value probably falls between these ranges and closer to the lesser values. The similarity of these estimates to the observed global extant spider family richness (110) is justification for using spiders in ecological studies, because it can be argued that Araneae are very well known at this taxonomic level on a global scale.

РЕЗЮМЕ. При условии сохранения скорости глобальных изменений и вымирания видов, задача по оценке глобального биоразнообразия нуждается в правильном анализе и экстраполяции данных инвентаризаций. Глобальное богатство семейств пауков оценено новым способом при помощи существующих методов экстраполяции и используя данные по количеству описанных семейств пауков по годам, что трактуется как прирастающие единицы знаний. Для независимой оценки, был применен новейший подход, обобощающий палеонтологические и неонтологические данные. Исходя из существующих методов, самые низкие обобщенные оценки глобального богатства семейств пауков варьируют между 110–112. Высшее обобщенное значение равняется 124. Реальное число, вероятно, находится где-то между этими значениями и ближе к нижнему из них. Сходство этих оценок с реально наблюдаемым глобальным богатством современных семейств пауков (110) является основанием для использования пауков в экологических исследованиях, поскольку можно утверждать, что Araneae очень хорошо изучены на этом таксономическом уровне в глобальном масштабе.

KEY WORDS: Araneae, fossils, extrapolative techniques, biodiversity, palaeontology.
КЛЮЧЕВЫЕ СЛОВА: Araneae, ископаемые, методы экстраполяции, биоразнообразие, палеонтология.

Introduction

The present rate of global climate change, habitat destruction through anthropogenic and other factors, and the subsequent rate of species extinctions means it is likely that many taxa will disappear before they have been scientifically described. In fact, Briggs [1991] likened the current episode of species demise to a present day mass extinction event. He suggested that

the rate of species loss is greater and more significant than the end-Cretaceous extinction that wiped out the dinosaurs and many other groups. To assess the consequences of this global change it is necessary to inventory as much of the global biota as possible, before components of it disappear forever. However, inventories of hyperdiverse taxa, such as spiders, from poorly studied and very diverse regions (such as tropical rainforests) can be problematic because of undersampling bias. Even intensive inventories of spiders from poorly studied regions are typically composed of a large number of singletons (species represented by only one specimen). Extrapolative estimates of total species richness from such data typically indicate that a large number of species have been missed. Colwell & Coddington [1994] reviewed the methods available for estimating terrestrial biodiversity through extrapolation.

A commonly used technique for estimating the number of taxa in a region is to extrapolate from species accumulation curves. A species accumulation curve (or collector's curve) is a plot of the cumulative number of species discovered, within a defined area, as a function of some measure of the effort expended to find them [Colwell & Coddington, 1994]. The prediction is based on the assumption that a finite number of taxa exists in the unit being studied, and that as sampling proceeds and the number of taxa found increases, the number of new taxa found will decrease [Caprariis *et al.*, 1981]. Thus, the cumulative species curve has a limiting value, i.e., the total richness, which it approaches asymptotically. If the values in the equation are inverted, a linear relationship between the inverses of the variables can be used to determine the total expected richness value based on the equation for a rectangular hyperbola [Caprariis *et al.*, 1981].

Palaeontologists face an additional problem in that the fossil record at species level can be very poor. Many species cannot be counted because they have not been fossilized. Higher taxa (e.g., families) are more likely to be preserved since there is more likelihood that one of their component species will be fossilized. However, analyses based on supraspecific taxa may produce erroneous results because of the lower degree of taxonomic resolution [see Penney,

2002a]. There are data for a range of organisms which demonstrate that family- and (in particular) genus-level diversities are good indicators of underlying species diversity [Lee, 1997]. Labandeira & Sepkoski [1993] justified the use of family data for fossil insects, on the following grounds: (1) this taxonomic rank appeared to correlate well with underlying species diversity in other studies of fossil diversity; (2) families are less prone to irregular and biased sampling than are fossil species and genera; (3) extant insect families are reasonably well established through consensus among taxonomists but this is often untrue for fossil species and genera; (4) insect families possess discrete, often highly stereotyped life habits, which can be informative in numerous palaeontological investigations. In this paper I make the assumption that the same is true for spiders.

Palaeontological and neontological data can be combined in the form of an evolutionary or phylogenetic tree. These trees are constructed by superimposing well-supported and accepted cladograms of hypothesized phylogenetic relationships, derived from work on extant taxa, over stratigraphic data from the fossil record [Smith, 1994]. Three assumptions are made when constructing these trees: (1) the cladogram is robust and provides the best available evidence for phylogenetic relationships of the taxa; (2) demonstrably monophyletic taxa have not given rise to other taxa; (3) stratigraphic range extensions should be kept to a minimum.

The known ranges provided by the fossil taxa, and the subsequent range extensions (the extra stratigraphic range added to the observed range of a taxon to make the evolutionary tree concordant with the phylogenetic hypotheses) of sister taxa and ghost lineages (a hypothetical branch of an evolutionary tree with no fossil data) and proposed ancestral lineages (which result from the addition of fossil metataxa [fossil taxa that are diagnosable, but which lack apomorphies], show the evolutionary history of a group over geological time. This technique, fully explained by Smith [1994] provides minimum dates for the hypothesized sister taxa dichotomies, and provides a graphical representation of the origination, extinction and divergence events of taxa through geological time.

In this paper, I employ the traditional cumulative species curve technique as a 'growth of knowledge curve' to estimate the total global number of extant spider families. This is compared with a novel technique, which provides a quantitative estimation based on Recent phylogenetic and palaeontological data in the form of an evolutionary tree.

Methods

The growth of knowledge curve

The cumulative number (cum N) of known spider families was plotted against date of description (obtained from Platnick [2002]; see also Marusik & Lehtinen [2003]) for the 110 currently accepted spider families (Appendix). The authorship year data were converted to 'incremental knowledge' units ranging from one (for the date of the first spider family description, i.e., 1833) to 169 (for the most recent year that a spider family was described, i.e., 2001). Inverse cum N was plotted against inverse incremental knowledge unit and a least squares regression applied. To eliminate any abnormality of curve shape due to accumulation order [e.g., Colwell & Coddington, 1994] an additional analysis using Colwell [1997], which employs various estimators (for a list see Table 1), was computed with 100 randomizations of the data. The input data file spreadsheet consisted of 34 803 cells and was entered as species, sample, abundance triplicates [see Colwell, 1997].

The evolutionary tree

The cladograms used here to produce the phylogenetic tree for spiders are based on Coddington & Levi [1991], with amendments, e.g., Griswold [1993], Scharff & Coddington [1997] and Griswold *et al.* [1998, 1999]. The minor changes to this phylogeny, suggested by Schütt [2000] are not included here. The cladograms were superimposed over geological time and calibrated using fossil data. The known ranges of spider families are based on the oldest described fossils (see figure legends for references). For detailed information on the construction of evolutionary trees see Smith [1994]. The

number of spider families known from described fossils over geological time were counted. These figures were compared against expected family palaeodiversity predicted from the presence of sister taxa at the point in geological time at which a particular family appears according to the proposed cladogram. Both observed and predicted family palaeodiversity data were plotted over geological time, subjected to regression analysis and the slopes and intercepts compared using ANCOVA.

Results and discussion

Supraspecific ranking is arbitrary and for any of the extrapolations presented to hold, the 'mindset' or social conventions among arachnological taxonomists would have to continue unchanged. However, they have been changing and will continue to do so. The number of spider families has increased dramatically since Simon, mostly because of ranking, not recognition. In addition, many family names have been proposed and are now in synonymy, even though some no doubt apply to monophyletic groups. Therefore, a background assumption of arachnological taxonomic 'social stasis' is essential for the accuracy of the predictions presented below to hold true in the future. As stated above, this will not happen and what is presented are predictions based on our current concepts of classification at this particular point in time.

The growth of knowledge curve estimates

Fig. 1 shows the 'growth of knowledge' curve for the description of extant spider families over time and Fig. 2, a least squares regression on the inverses of these values. The estimated value for extant spider richness, based on these data is 44.25. Fig. 3 shows the growth of knowledge curve using 100 randomizations of the data. Total family richness estimates based on these data range from 110–112 (Table 1).

The curve for cumulative number of spider families described over time (Fig. 1) does not fit the expected pattern for a standard cumulative species curve. In fact, the curve seems to
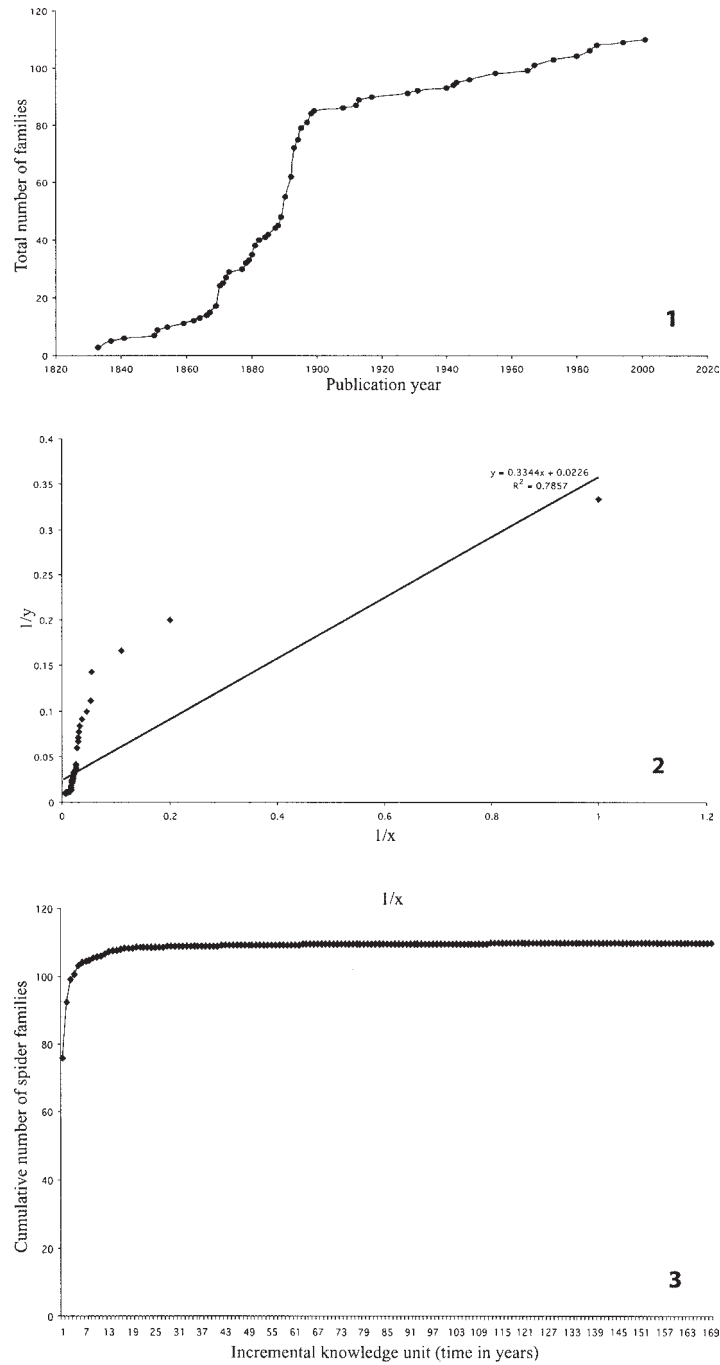
Figs 1–3. Spider family date description analyses: 1 — cumulative number of described extant spider families plotted over year of authorship; 2 — least squares regression on the inverses of the dependent and independent variables from Fig. 1; 3 — cumulative number of described extant spider families plotted over incremental knowledge units (time in years) after 100 randomizations of the data.

Рис. 1–3. Анализ данных по описанию семейств пауков: 1 — общее количество описанных современных семейств пауков против годов их опубликования; 2 — линейная регрессия (в смысле наименьшего квадратичного отклонения) обратных величин этих значений, взятых из Рис. 1; 3 — кривая роста знаний (время в годах), использующая выборку из 100 случайных значений этих данных.

Extant spider family richness estimates derived from Fig. 3 using Colwell [1997].
Богатство современных семейств пауков по оценке данных из Рис. 3, используя Colwell [1997].

Statistical estimation model (see Colwell [1997] for details and references)	Estimate
Abundance-based coverage estimator of species richness	111.09
Incidence-based coverage estimator of species richness	110.93
Chao 1 richness estimator	110.5
Chao 2 richness estimator	110.5
First-order Jackknife richness estimator	110.99
Second-order Jackknife richness estimator	111.98
Bootstrap richness estimator	110.37
Michaelis-Menten richness estimator (over randomizations)	109.94
Michaelis-Menten richness estimator (computed once over mean curve)	110.2

represent two different functions that intersect at around the year 1889. I consider this an artefact caused by the rules set out for naming animal taxa in the ICZN [1999]. Article 36 states that a name established for a taxon at any rank in the family group has the same authorship and date at every rank. This means that although a number of taxa were given family status during the twentieth century they are attributed to authors in the nineteenth, who had previously established them as subfamilies. This would make these samples artificially richer than they actually are. For example, the family Periegopidae was elevated to family rank by Forster [1995] but is still attributed to Simon [1893], more than a century earlier. When rich samples are added earlier they tend to cause a more pronounced shoulder and earlier asymptote in the accumulation curve [Coddington *et al.*, 1996], which is certainly the case here (Fig. 1) and explains the low value for predicted spider family richness.

The curve obtained after randomizing the data 100 times (Fig. 3) conforms to the expected pattern for the standard cumulative species curve and is therefore, considered more accurate. For completeness, all richness estimates produced using [Colwell, 1997] are given in Table 1. The extrapolated values for global spider family richness using these different models range from 110 to 112. By its very nature, extrapolation multiplies bias as well as case-to-case random error and different models may prove to be more effective for different animal groups or datasets [Colwell & Coddington, 1994]. However, these estimators have been little used in the ecological literature and it would be premature to make firm recommendations as to their use [Colwell, 1997].

The evolutionary tree estimates

Figs 4 and 5 show the evolutionary history of Araneae over time. These provided the data (Table 2) for construction of the spindle diagrams of observed and expected spider family diversity through geological time (Fig. 6). Regression analyses and ANCOVA on the observed and predicted data (Fig. 7) demonstrate no significant difference between the slopes of the lines ($t = -0.8942$, df = 39, P > 0.1), but show a highly significant difference between the intercepts of the lines ($t = -7.4469$, df = 40, P < 0.0001). The observed data predicts a total expected extant family richness of 54, whereas the predicted data proposes 124 families.

The increase of a taxon's diversity over time is essentially a Markovian process, i.e., the newly evolved taxa are dependent on the presence of the ancestral taxa. Thus, the number of new taxa at any time is dependent, in part, upon the number of existing taxa. Therefore, the null model for the diversification process of a radiating group is a sigmoid curve with exponential increase, and the logarithm of its diversity plot during the incremental phase will form a straight-line regression function of geological time [Sepkoski, 1979]. This is seen in both observed and predicted spider family palaeodiversities (Fig. 7) and the similarity of the slopes indicates that the rate of change is the same in both cases. However, as noted earlier there is a highly significant difference between the intercepts of
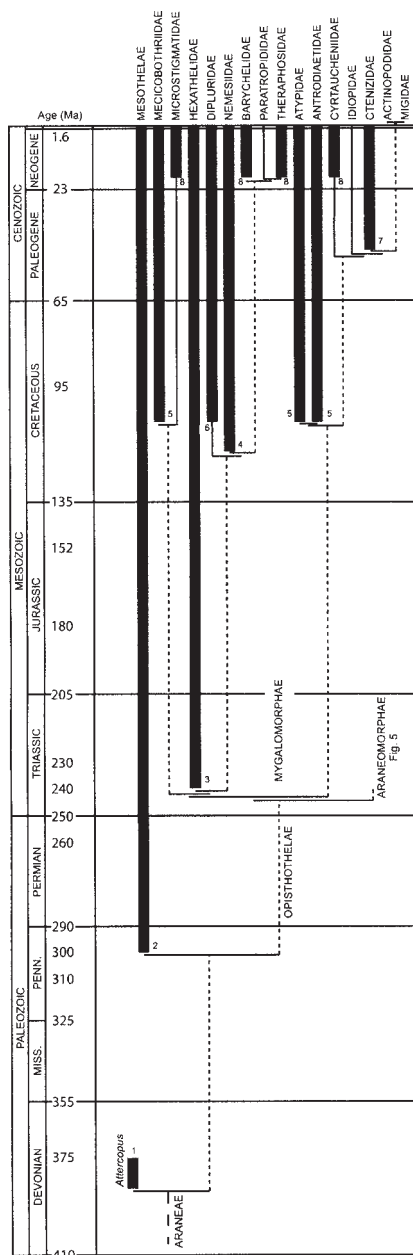
Fig. 4. Evolutionary tree of the spider suborders Mesothelae and Mygalomorphae (for key see Fig. 5). References: 1 — Selden *et al*. [1991]; 2 — Selden [1996]; 3 — Selden & Gall [1992]; 4 — Selden [2002]; 5 — Eskov & Zonstein [1990]; 6 — Selden *et al*. [2002]; 7 — Wunderlich [2000]; 8 — Wunderlich [1988].

Рис. 4. Эволюционное дерево отрядов пауков Mesothelae и Mygalomorphae (ключ на Рис. 5). Ссылки: 1 — Selden *et al*. [1991]; 2 — Selden [1996]; 3 — Selden & Gall [1992]; 4 — Selden [2002]; 5 — Eskov & Zonstein [1990]; 6 — Selden *et al*. [2002]; 7 — Wunderlich [2000]; 8 — Wunderlich [1988].

the lines. The predicted value of 124 extant families is much closer to the actual value (110) [e.g., Platnick, 2002; see Marusik & Lehtinen, 2003 for an additional family] than that produced by the regressions on the observed data (54). It is entirely feasible that ten or so families remain to be discovered or newly erected, which would more closely approximate the predicted value. However, this value was obtained by extending the exponential regression line from 20 Ma (the most Recent data point; Dominican Republic amber) until present. This pattern of diversification, if left unconstrained would tend towards infinity [Sepkoski, 1979], which is clearly absurd. The line will reach an asymptote once the maximum spider family diversity sustainable by the constraints of the biosphere has been reached. Although this is a relatively short extension of the line, the predicted value can be expected to be slightly lower in reality.

Ideally, we would have a complete knowledge of global spider family richness and a complete fossil record. In the latter case, the observed and predicted regression lines in Fig. 7 would merge into a single line. In addition, some function of these data would intercept the y axis at a value equal to, or extremely close to the actual number of families observed at 0 Ma, i.e., the extant global spider family richness. For both observed and predicted slopes, the presence of extinct families late in the fossil record may elevate the y intercept to a value slightly above the actual value of extant families. Extinct families early in the fossil record may lower the intercept. These limitations need to be considered when combining these data for this purpose. At present there is a significant difference in the intercepts of the observed and predicted lines. As our knowledge of the fossil record increases, the intercept of the observed line can be expected to increase at a much quicker rate than the predicted. It is also possible for the predicted line to fall slightly if the structure of the cladogram changes. Future discoveries of families in the Palaeozoic and Mesozoic might reduce the slope of the observed and predicted lines. Under these circumstances, the y intercept of the predicted line would be lower than at present and thus closer to the lower bound estimates provided by the growth of knowledge curve analysis.
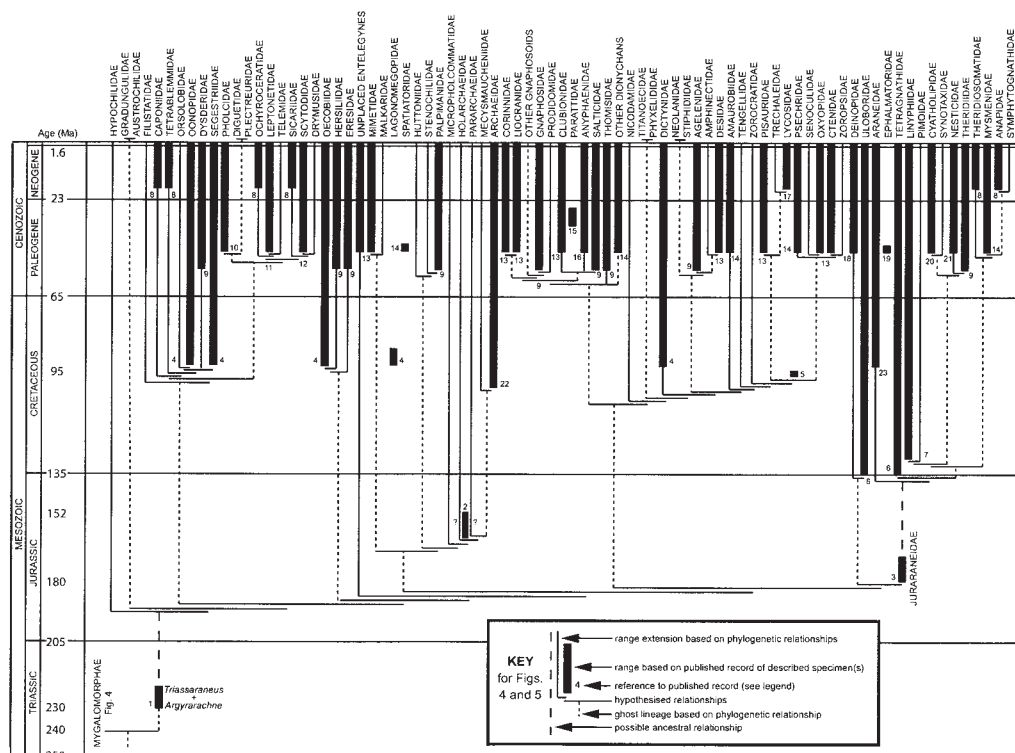
Fig. 5. Evolutionary tree of the spider suborder Araneomorphae. Other gnaphosoids include: Gallieniellidae, Ammoxenidae, Cithaeronidae, Trochanteriidae and Lamponidae; other dionychans include: Zoridae, Selenopidae, Sparassidae and Philodromidae [see Coddington & Levi, 1991]; unplaced entelegynes include: Cryptothelidae, Cybaeidae, Cycloctenidae, Hahniidae, Halidae, Homalonychidae, Miturgidae and Zodariidae [see Griswold *et al.*, 1999] and Chummidae [Jocqué, 2001]. References: 1 — Selden *et al.* [1999]; 2 — Eskov [1987]; 3 — Eskov [1984]; 4 — Penney [2002b]; 5 — Rayner & Dippenaar-Schoeman [1995]; 6 — Selden & Penney [2003], Selden [1990]; 7 — Penney & Selden [2002]; 8 — Wunderlich [1988]; 9 — Gourret [1888]; 10 — Menge [1869]; 11 — Wunderlich [1991]; 12 — Wunderlich [1993a]; 13 — Petrunkevitch [1958]; 14 — Petrunkevitch [1942]; 15 — Petrunkevitch [1922]; 16 — Petrunkevitch [1946]; 17 — Penney [2001]; 18 — Wunderlich [1986]; 19 — Petrunkevitch [1950]; 20 — Wunderlich [1993b] (see also Griswold [2001]); 21 — Eskov & Marusik [1992]; 22 — Penney [2003]; 23 — Penney [2004]. A complete review of the spider fossil record which will plot all known fossil occurrences of fossil spiders on the evolutionary tree is in preparation.

Рис. 5. Эволюционное дерево подотрядов пауков Araneomorphae. Другие гнафозоиды включают: Gallieniellidae, Ammoxenidae, Cithaeronidae, Trochanteriidae и Lamponidae; другие диониха включают: Zoridae, Selenopidae, Sparassidae и Philodromidae [см. Coddington & Levi, 1991]; отдельностоящие энтелегины: Cryptothelidae, Cybaeidae, Cycloctenidae, Hahniidae, Halidae, Homalonychidae, Miturgidae и Zodariidae [см. Griswold *et al.*, 1999] и Chummidae [Jocqué, 2001]. 1 — Selden *et al.* [1999]; 2 — Eskov [1987]; 3 — Eskov [1984]; 4 — Penney [2002b]; 5 — Rayner & Dippenaar-Schoeman [1995]; 6 — Selden & Penney [2003], Selden [1990]; 7 — Penney & Selden [2002]; 8 — Wunderlich [1988]; 9 — Gourret [1888]; 10 — Menge [1869]; 11 — Wunderlich [1991]; 12 — Wunderlich [1993a]; 13 — Petrunkevitch [1958]; 14 — Petrunkevitch [1942]; 15 — Petrunkevitch [1922]; 16 — Petrunkevitch [1946]; 17 — Penney [2001]; 18 — Wunderlich [1986]; 19 — Petrunkevitch [1950]; 20 — Wunderlich [1993b] (см. также Griswold [2001]); 21 — Eskov & Marusik [1992]; 22 — Penney [2003]; 23 — Penney [2004]. Полный обзор ископаемых находок пауков, который будет включать все известные находки ископаемых пауков по эволюционному дереву, готовится.

Conclusions

This research was initiated primarily as a strictly academic exercise driven by my own curiosity. However, certain outcomes are of broader interest. For example, the predicted spider family palaeodiversity based on the evolutionary tree data is considered more accurate than the observed, because of its close similarity at 0 Ma to the actual number of extant spider
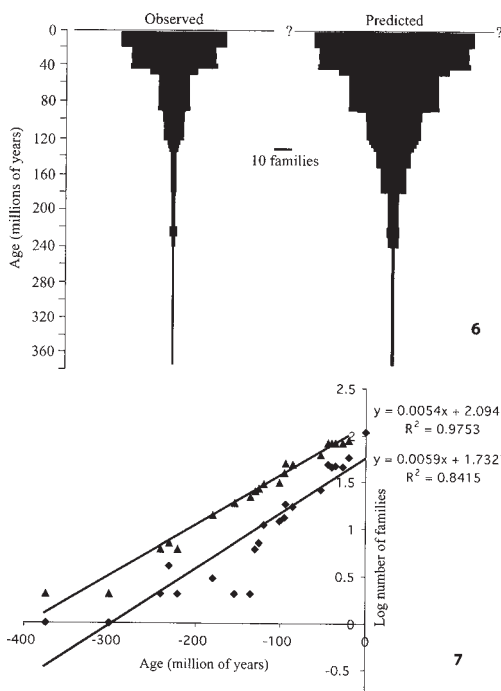
Table 2.
Spider family palaeodiversity data derived from the evolutionary tree. Ma = age in millions of years, Obs = observed, Pre = predicted.

Таблица 2.
Палеоразнообразие семейств пауков исходя из данных по эволюционному дереву. Ma = возраст в миллионах лет, Obs = наблюдаемое, Pre = предполагаемое.

Ma	375	300	240	230	220	180	154	135	130	125	120	101	95	94	86	53	44	40	35	27	20	0
Obs	1	1	2	4	2	3	3	5	6	7	11	12	13	18	17	26	48	46	47	46	58	110
Pre	2	2	6	7	6	14	19	22	25	27	30	31	40	50	49	61	84	82	83	82	88	—

Figs 6–7. Data and analyses derived from the evolutionary tree: 6 — spindle diagrams of observed and predicted spider family paleodiversity based on data derived from the evolutionary tree and presented in Table 2; 7 — linear regression plots of observed and predicted spider family richness over geological time. Triangle = predicted, diamond = observed.

Рис. 6–7. Данные и анализ исходя из эволюционного дерева: 6 — веретенообразные диаграммы известного и предсказанного палеоразнообразия семейств пауков, на основе данных эволюционного дерева и данных таблицы 2; 7 — плот линейной регрессии известного и предсказанного богатства семейств пауков по ходу геологического времени. Треугольники = предсказано, ромбы = известно.

families. This highlights the importance of combining neontological and palaeontological data in a phylogenetic context in such investigations. It also demonstrates that our current palaeoarachnological knowledge is limited and calls for further research in this subject area. The upper bound estimate is only 12.7% over the observed and this figure should drop as new extant spider families are identified and as our palaeoarachnological dataset increases.

References

Briggs J.C. 1991. A Cretaceous-Tertiary mass extinction? Were most of Earth's species killed off? // BioScience. Vol.41. P.619–624.

Caprariis P. de, Lindemann R. & Haimes R. 1981. A relationship between sample size and accuracy of species richness predictions // Math. Geol. Vol.13. P.351–355.

Coddington J.A. & Levi H.W. 1991. Systematics and evolution of spiders (Araneae) // Ann. Rev. Ecol. Syst. Vol.22. P.565–592.

Coddington J.A., Young L.H. & Coyle F.A. 1996. Estimating spider species richness in a southern Appalachian cove hardwood forest // J. Arachnol. Vol.24. P.111–128.

Colwell R.K. 1997. EstimateS: Statistical estimation of species richness and shared species from samples. Version 5 // User's guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Colwell R.K. & Coddington J.A. 1994. Estimating terrestrial biodiversity through extrapolation // Phil. Trans. Roy. Soc. Lond., Series B. Vol.345. P.101–118.

Eskov K.Yu. 1984. A new fossil spider family from the Jurassic of Transbaikalia (Araneae, Chelicerata) // Neues Jahrbuch Geol. Paläontol., Monatshefte. Hft.1984. S.645–653.

Eskov K.Yu. 1987. A new archaeid spider (Chelicerata, Araneae) from the Jurassic of Kazakhstan, with notes on the so-called 'Gondwanan' ranges of Recent taxa // Neues Jahrbuch Geol. Paläontol. Abhandl. Bd.175. Hft.1. S.81–106.

Eskov K.Yu. & Marusik YU.M. 1992. Fossil spiders of the family Nesticidae (Chelicerata, Araneida) // Paleontol. Zhur. Vol.2. P.87–95 [in Russian, with English abstract].

Eskov K.Yu. & Zonstein S.L. 1990. First Mesozoic mygalomorph spiders from the Lower Cretaceous of Sibe-

ria and Mongolia, with notes on the system and evolution of the infraorder Mygalomorphae (Chelicerata, Araneae) // Neues Jahrbuch Geol. Paläontol. Abhandl. Bd.178. Hft.3. S.325–368.

Forster R.R. 1995. The Australasian spider family Periegopidae Simon, 1893 (Araneae: Sicarioidea) // Rec. West. Aust. Mus. Suppl. number 52. P.91–105.

Gourret M.P. 1888. Recherches sur les arachnides Tertiaires d'Aix en Provence // Rec. Zool. Suisse. Vol.1888. P.431–496.

Griswold C.E. 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida, Araneae, Lycosoidea) // Smithson. Contr. Zool. Vol.539. P.1–39.

Griswold C.E. 2001. A monograph of the living world genera and afrotropical species of cyatholipid spiders (Araneae, Orbiculariae, Araneoidea, Cyatholipidae) // Mem. Calif. Acad. Sci. Vol.26. P.1–251.

Griswold C.E., Coddington J.A., Hormiga G. & Scharff N. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea) // Zool. J. Linn. Soc. Vol.123. P.1–99.

Griswold C.E., Coddington J.A., Platnick N.I. & Forster R.R. 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae) // J. Arachnol. Vol.27. P.53–63.

ICZN. 1999. International code of zoological nomenclature (4th edn.). London: The International Trust for Zoological Nomenclature. 306 p.

Jocqué R. 2001. Chummidae, a new spider family (Arachnida: Araneae) from South Africa // J. Zool., Lond. Vol.254. P.481–493.

Labandeira C.C. & Sepkoski J.J. Jr. 1993. Insect diversity in the fossil record // Science. Vol.261. P.310–315.

Lee M.S.Y. 1997. Documenting present and past biodiversity: conservation biology meets palaeontology // Tr. Ecol. Evo. Vol.12. P.132–133.

Marusik Yu.M. & Lehtinen P.T. 2003. Synaphridae Wunderlich, 1986 (Aranei, Araneoidea), a new family status, with a description of a new species from Turkmenistan // Arthropoda Sel. Vol.11. P.159–165.

Penney D. 2001. Advances in the taxonomy of spiders in Miocene amber from the Dominican Republic // Palaeontology. Vol.44. P.987–1009.

Penney D. 2002a. Paleoecology of Dominican amber preservation: spider (Araneae) inclusions demonstrate a bias for active, trunk-dwelling faunas // Paleobiology. Vol.28. P.389–398.

Penney D. 2002b. Spiders in Upper Cretaceous amber from New Jersey (Arthropoda: Araneae) // Palaeontology. Vol.45. P.709–724.

Penney D. 2003. *Afrarchaea grimaldii,* a new species of Archaeidae (Araneae) in Cretaceous Burmese amber // J. Arachnol. Vol.31. P.122–130.

Penney D. 2004. New spiders in Upper Cretaceous amber from New Jersey in the American Museum of Natural History (Arthropoda, Araneae) // Palaeontology. Vol.47. P.367–375.

Penney D. & Selden P.A. 2002. The oldest linyphiid spider, in Lower Cretaceous Lebanese amber (Araneae, Linyphiidae, Linyphiinae) // J. Arachnol. Vol.30. P.487–493.

Petrunkevitch A. 1922. Tertiary spiders and opilionids of North America // Trans. Conn. Acad. Arts Sci. Vol.25. P.211–279.

Petrunkevitch A. 1942. A study of amber spiders // Trans. Conn. Acad. Arts Sci. Vol.34. P.119–464.

Petrunkevitch A. 1946. Fossil spiders in the collection of the American Museum of Natural History // Am. Mus. Novit. Vol.1328. P.1–36.

Petrunkevitch A. 1950. Baltic amber spiders in the Museum of Comparative Zoology // Bull. Mus. Comp. Zool. Harv. Vol.103. P.259–337.

Petrunkevitch A. 1958. Amber spiders in European collections // Trans. Conn. Acad. Arts Sci. Vol.41. P.97–400.

Platnick N.I. 2002. The world spider catalog, version 3.0. // American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog81-87/index.html

Rayner R.J. & Dippenaar-Schoeman A.S. 1995. A fossil spider (superfamily Lycosoidea) from the Cretaceous of Botswana // S. Afr. J. Sci. Vol.91. P.98–100.

Scharff N. & Coddington J.A. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae) // Zool. J. Linn. Soc. Vol.120. P.355–434.

Schütt K. 2000. The limits of the Araneoidea (Arachnida: Araneae) // Aus. J. Zool. Vol.48. P.135–153.

Selden P.A. 1990. Lower Cretaceous spiders from the Sierra del Montsech, north-east Spain // Palaeontology. Vol.33. P.257–285.

Selden P.A. 1996. First fossil mesothele spider, from the Carboniferous of France // Rev. Suisse Zool. (Vol. Hors Série). P.585–596.

Selden P.A. 2002. First British Mesozoic spider, from Cretaceous amber of the Isle of Wight // Palaeontology. Vol.45. P.973–983.

Selden P.A. & Gall J.-C. 1992. A Triassic mygalomorph spider from the northern Vosges, France // Palaeontology. Vol.35. P.211–235.

Selden P.A. & Penney D. 2003. Lower Cretaceous spiders (Arthropoda: Arachnida: Araneae) from Spain // Neues Jahrbuch Geol. Paläontol. Abhandl. Bd.2003. S.175–192.

Selden P.A., Shear W.A. & Bonamo P.M. 1991. A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae // Palaeontology. Vol.34. P.241–281.

Selden P.A., Anderson H.M. Anderson J.M. & Fraser N.C. 1999. The oldest araneomorph spiders, from the Triassic of South Africa and Virginia // J. Arachnol. Vol.27. P.401–414.

Selden P.A., Casado F. da C. & Mesquita M.V. 2002. Funnel-web spiders (Araneae: Dipluridae) from the Lower Cretaceous of Brazil // Boletim do 6 Simpósio sobre o Cretácio do Brasil. 2 Simpósio sobre el Cretácico de América del Sur (2002). P.89–91.

Sepkoski J.J. Jr. 1979. A kinetic model of Phanerozoic taxonomic diversity II. Early Phanerozoic families and multiple equilibria // Paleobiology. Vol.5. P.222–251.

Simon E. 1893. Histoire Naturelle des Araignées. Paris: Encyclopédie Roret. Vol.2. No.1. P.257–488.

Smith A.B. 1994. Systematics and the fossil record: documenting evolutionary patterns. Oxford: Blackwell Science. 223 p.

Wunderlich J. 1986. Spinnenfauna gestern und heute. Fossile Spinnen in Bernstein und ihre heute lebenden Verwandten. Wiesbaden: Erich Bauer Verlag bei Quelle und Meyer. 283 S.

Wunderlich J. 1988. Die fossilen Spinnen im Dominikanischen Bernstein // Beitr. Araneol. Bd.2. S.1–378.

Wunderlich J. 1991. Beschreibung der ersten fossilen Spinne der Familie Leptonetidae: *Eoleptoneta kutscheri* n.gen., n.sp. in Sächsischem Bernstein (Arach-nida, Araneae) // Entomol. Z. Bd.101. S.21–25.

Wunderlich J. 1993a. Die ersten fossilen Becherspinnen (Fam. Cyatholipidae) in Baltischem und Bitterfelder Bernstein (Arachnida, Araneae) // Mitt. Geol. Paläontol. Inst. Univ. Hamburg. Hft.75. S.231–241.

Wunderlich J. 1993b. Die ersten fossilen Speispinnen (Fam. Scytodidae) im Baltischen Bernstein (Arachnida, Araneae) // Mitt. Geol. Paläontol. Inst. Univ. Hamburg. Hft.75. S.243–247.

Wunderlich J. 2000. Zwei neue Arten der Familie Falltürspinnen (Araneae: Ctenizidae) aus dem Baltischen Bernstein // Entomol. Z. Bd.110. S.345–348.

Appendix.

Spider families and authorships, listed chronologically by year of publication (from Platnick [2002], except for Synaphridae, see Marusik & Lehtinen [2003]). The individual references are not provided in the reference list unless they occur in the main body of the text.

Theridiidae Sundevall, 1833; Lycosidae Sundevall, 1833; Thomisidae Sundevall, 1833; Dysderidae C.L. Koch, 1837; Agelenidae C.L. Koch, 1837; Salticidae Blackwall, 1841; Deinopidae C.L. Koch, 1850; Pholcidae C.L. Koch, 1851; Eresidae C.L. Koch, 1851; Archaeidae C.L. Koch et Berendt 1854; Linyphiidae Blackwall, 1859; Oecobiidae Blackwall, 1862; Scytodidae Blackwall, 1862; Tetragnathidae Menge, 1866; Filistatidae Ausserer, 1867; Liphistiidae Thorell, 1869; Uloboridae Thorell, 1869; Atypidae Thorell, 1870; Theraphosidae Thorell, 1870; Palpimanidae Thorell, 1870; Hersiliidae Thorell, 1870; Oxyopidae Thorell, 1870; Amaurobiidae Thorell, 1870; Philodromidae Thorell, 1870; Dictynidae O. Pickard-Cambridge, 1871; Cryptothelidae L. Koch, 1872; Sparassidae Bertkau, 1872; Tetrablemmidae O. Pickard-Cambridge, 1873; Stenochilidae Thorell, 1873; Ctenidae Keyserling, 1877; Hahniidae Bertkau, 1878; Anyphaenidae Bertkau, 1878; Trochanteriidae Karsch, 1879; Sicariidae Keyserling, 1880; Corinnidae Karsch, 1880; Mimetidae Simon, 1881; Theridiosomatidae Simon, 1881; Zodariidae Thorell, 1881; Mecicobothriidae Holmberg, 1882; Zoropsidae Bertkau, 1882; Prodidomidae Simon, 1884; Miturgidae Simon, 1885; Ctenizidae Thorell, 1887; Clubionidae Wagner, 1887; Hypochilidae Marx, 1888; Dipluridae Simon, 1889; Barychelidae Simon, 1889; Paratropididae Simon, 1889; Leptonetidae Simon, 1890; Caponiidae Simon, 1890; Oonopidae Simon, 1890; Trechaleidae Simon, 1890; Pisauridae Simon, 1890; Senoculidae Simon, 1890; Psechridae Simon, 1890; Hexathelidae Simon, 1892; Cyrtaucheniidae Simon, 1892; Idiopidae Simon, 1892; Actinopodidae Simon, 1892; Migidae Simon, 1892; Nemesiidae Simon, 1892; Cybaeidae Banks, 1892; Periegopidae Simon, 1893; Drymusidae Simon, 1893; Plectreuridae Simon, 1893; Segestriidae Simon, 1893; Huttoniidae Simon, 1893; Homalonychidae Simon, 1893; Ammoxenidae Simon, 1893; Cithaeronidae Simon, 1893; Lamponidae Simon, 1893; Zoridae F.O. Pickard-Cambridge, 1893; Cyatholipidae Simon, 1894; Synotaxidae Simon, 1894; Nesticidae Simon, 1894; Mecysmaucheniidae Simon, 1895; Anapidae Simon, 1895; Araneidae Simon, 1895; Desidae Pocock, 1895; Liocranidae Simon, 1897; Selenopidae Simon, 1897; Cycloctenidae Simon, 1898; Nicodamidae Simon, 1898; Gnaphosidae Pocock, 1898; Diguetidae F.O. Pickard-Cambridge, 1899; Tengellidae Dahl, 1908; Ochyroceratidae Fage, 1912; Telemidae Fage, 1912; Zorocratidae Dahl, 1913; Stiphidiidae Dalmas, 1917; Mysmenidae Petrunkevitch, 1928; Symphytognathidae Hickmann, 1931; Antrodiaetidae Gertsch, 1940; Microstigmatidae Roewer, 1942; Micropholcommatidae Hickman 1943; Gallieniellidae Millot, 1947; Austrochilidae Zapfe, 1955; Gradungulidae Forster, 1955; Orsolobidae Cooke, 1965; Phyxelididae Lehtinen, 1967; Titanoecidae Lehtinen, 1967; Neolanidae Forster et Wilton, 1973; Amphinectidae Forster et Wilton, 1973; Malkaridae Davies, 1980; Pararchaeidae Forster and Platnick, 1984; Holarchaeidae Forster and Platnick, 1984; Pimoidae Wunderlich, 1986; Synaphridae Wunderlich, 1986 [see Marusik & Lehtinen 2003]; Halidae Jocqué, 1994; Chummidae Jocqué, 2001.