

Palaeontomology: towards the big picture

Edmund A. JARZEMBOWSKI

Received: 1 Feb., 2002

Accepted for publication: 1 June, 2002

JARZEMBOWSKI E. A. 2003. Palaeontomology: towards the big picture. *Acta zoologica cracoviensia*, **46**(suppl.– Fossil Insects): 25-36.

Abstract. Insects (Superclass Hexapoda) are the most palaeodiverse as well as the most biodiverse organisms of all time but probably total under 20 million species. Familial/generic data agree with an exponential growth model of the evolution of terrestrial life. Ordinal data is consistent with a logistic model but with a major perturbation superimposed (the Triassic extinction). The global taxonomic carrying capacity is about 31 for orders whereas familial and species data suggest power functions. Key events in the Phanerozoic insect record are briefly discussed.

Key words: insects, fossils, palaeodiversity, biodiversity, evolutionary patterns.

E. A. JARZEMBOWSKI, Maidstone Museum & Bentlif Art Gallery, St Faith's St., Maidstone, Kent, ME14 1LH and P.R.I.S., Reading University, UK.

E-mail: edjarzembowski@maidstone.gov.co.uk

I. BIODIVERSITY AND PALAEOODIVERSITY

Insects comprise well over 50 percent of global species biodiversity (Figs 1, 2). The description of new insect species is more or less exponential (Fig. 3). In contrast, the recognition of new insect orders is in decline (Fig. 4: total). The description of new insect orders peaked in the nineteenth century. This was mainly due to the impact of various living orders being erected (Fig. 4: extant). It remains possible, however, that more fossil orders will be recognised in the future (Fig. 4: extinct).

Some workers maintain that evolutionary change is best studied at the species level (WILLMANN 1997) but others consider that family databases are a good proxy (BENTON et al. 2000). At family level, insects are the most diverse group in the fossil record (BENTON 1993: fig. P.2). Trend lines based on family palaeodiversity suggest that insects total under 20 million species (JARZEMBOWSKI & ROSS 1993: Fig. 9; this paper, Fig. 10). This agrees with the current tendency by entomologists to estimate a total of less than the 50 or even 100 million species proposed during the heyday of Erwinian estimates.

A c k n o w l e d g e m e n t s. I wish to thank Prof. M. BENTON (Bristol University) and Mr R. CORAM (Reading University) for some copies of papers consulted and Drs A. GOROKHOV (Zoological Institute, Russian Academy of Sciences), W. KRZEMIŃSKI (Natural History Museum, Polish Academy of Sciences), C. LABANDEIRA (Dept. of Paleobiology, National Museum of Natural History, Smithsonian Institution), A. NEL (Entomology Laboratory, National Museum of Natural History, Paris) and D. SHCHERBAKOV (Arthropod Laboratory, Palaeontological Institute, Russian Academy of Sciences) for comments towards Fig. 10. This is P.R.I.S. contribution.

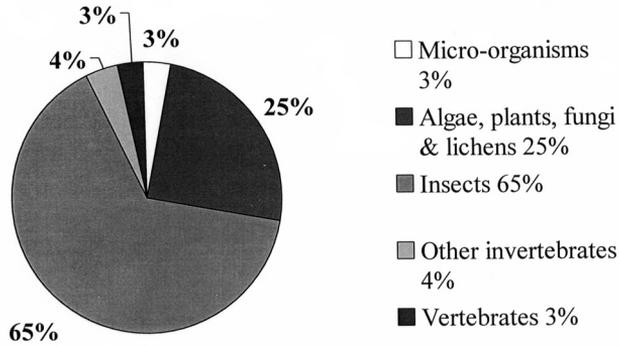


Fig. 1. Global biodiversity based on known species (approximately 1.454 million). After CRANBROOK (1996), WILSON (1992).

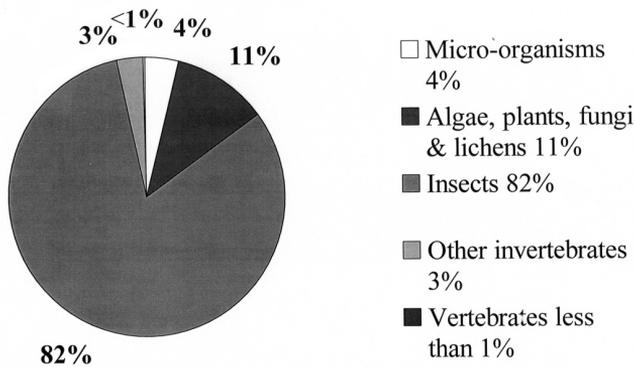


Fig. 2. Estimated global biodiversity (approximately 65.654 million). Based on references in Fig. 1.

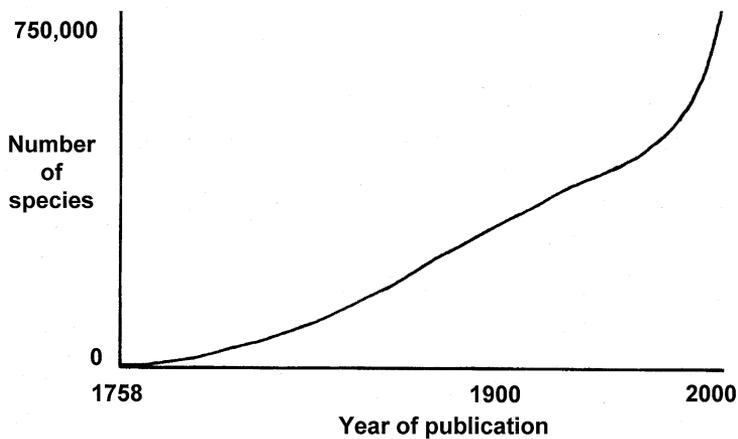


Fig. 3. Rate of description of insect species. After BENTON (2001).

Table I

Time ranges of insect orders

1.	Protura SILVESTRI, 1907*	–	R
2.	Collembola LUBBOCK, 1871*	springtails	D1-R
3.	Diplura BÖRNER, 1904*	two-pronged bristletails	C2-R
4.	Archaeognatha BÖRNER, 1904*	bristletails	D2?-R
5.	Monura SHAROV, 1951*	–	C2-P
6.	Zygentoma BÖRNER, 1904*	silverfish	C2-R
7.	Palaeodictyoptera GOLDENBERG, 1877* + Permothemistida SINITSHENKOVA, 1980.	–	C2-P2
8.	Megasecoptera BRONGNIART, 1885*	–	C2-P
9.	Diaphanopteroidea HANDLIRSCH, 1919*	–	C2-P
10.	Ephemeroptera HYATT & ARMS, 1890*	mayflies	C2-R
11.	Protodonata BRONGNIART, 1893*	‘giant dragonflies’	C2-Tr3
12.	Odonata FABRICIUS, 1793*	dragonflies	C2-R
13.	‘Protorthoptera’ HANDLIRSCH, 1906	–	C1-Tr
14.	Plecoptera BURMEISTER, 1838*	stoneflies	P1-R
15.	Embioptera SHIPLEY, 1904*	web-spinners	P1-R
16.	Phasmatodea BRUNNER, 1893*	stick insects	P2-R
17a.	Orthoptera OLIVIER, 1789*	crickets, grasshoppers, locusts	C2-R
17b.	Titanoptera SHAROV, 1968	–	Tr
18.	Grylloblattodea BRUES & MELANDER, 1915*	–	P1-R
19.	Protelytroptera TILLYARD, 1931	–	P
20.	Dermaptera DE GEER, 1773*	earwigs	J1-R
21.	Miomoptera MARTYNOV, 1927*	–	C2-J1
22.	Blattodea BRUNNER, 1882*	cockroaches	C2-R
23.	Isoptera BRULLÉ, 1832*	termites	K1-R
24.	Mantodea BURMEISTER, 1838*	praying mantises	K1-R
25.	Caloneuroidea HANDLIRSCH, 1937	–	C2-P
26.	Zoraptera SILVESTRI, 1913*	–	O-R
27.	Psocoptera SHIPLEY, 1904*	booklice	P1-R
28.	Phthiraptera HAECKEL, 1896*	lice	E-R
29.	Thysanoptera HALIDAY, 1836*	thrips	P1-R
30.	Hemiptera LINNÉ, 1758*	bugs	C2-R
31.	Glosselytroidea MARTYNOV, 1938	–	P1-J3
32.	Strepsiptera KIRBY, 1815*	stylopids	E-R
33.	Coleoptera LINNÉ, 1758*	beetles	P1-R
34.	Raphidioptera LATREILLE, 1810*	snake flies	P2-R
35.	Megaloptera LATREILLE, 1802*	alder flies	P1-R
36.	Neuroptera LINNÉ, 1758*	lacewings	P1-R
37.	Hymenoptera LINNÉ, 1758*	wasps, ants, bees	Tr3-R
38.	Trichoptera KIRBY, 1815*	caddisflies	P1-R
39.	Lepidoptera LINNÉ, 1758*	moths, butterflies	J1-R
40.	Diptera LINNÉ, 1758*	flies	Tr2-R
41.	Siphonaptera LATREILLE, 1825*	fleas	K1-R
42.	Mecoptera PACKARD, 1886*	scorpionflies	P1-R

Key: **D1**, Lower Devonian, ca 398 Ma; **D2**, Middle Devonian, ca 391 Ma; **C1**, Lower Carboniferous; **C2**, Upper Carboniferous, ca 307 Ma; **P**, Permian; **P1**, Lower Permian, ca 251 Ma; **P2**, Upper Permian, ca 273 Ma; **Tr**, Triassic; **Tr3**, Upper Triassic, ca 222 Ma; **J1** Lower Jurassic, ca 193 Ma; **J3**, Upper Jurassic, ca 151 Ma; **K1**, Lower Cretaceous, ca 121 Ma; **E**, Eocene, ca 46 Ma; **O**, Oligocene, ca 29 Ma; **R**, Recent, 0.01 Ma-.

* clades (DUNCAN, 1997 and references therein)

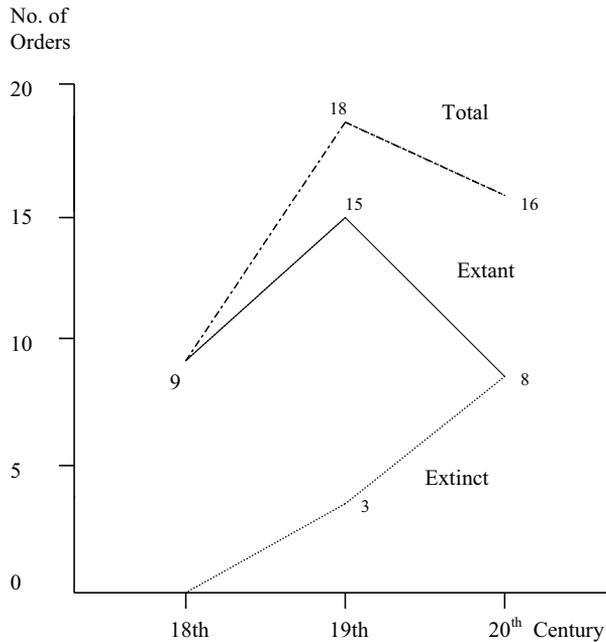


Fig. 4. Rate of description of insect orders: extinct (dotted line), extant (solid) and total (dotted-and-dashed). Data from Table I.

II. PHANEROZOIC PATTERNS

BENTON & HARPER (2000) suggested that there is a difference in style between evolution in land organisms as compared with evolution in the marine realm. They considered that terrestrial life has evolved exponentially whereas life in the sea has evolved logistically (cf. Fig. 5). Insects are crucial to this discussion because they are a significant element of terrestrial life (JARZEMBOWSKI 2001). Generic and familial data suggest exponential growth during the Phanerozoic (Figs 6, 7). In contrast, ordinal data suggest a logistic (sigmoidal) pattern but with a major perturbation superimposed – the Triassic extinction (Fig. 8). If the effect of the latter is subtracted, then ordinal diversity levels off at about 31 orders from a total of about 42 orders of insects.

BENTON (2001) considered that, in general, a logistic pattern at high taxonomic level could decay into an exponential pattern at low taxonomic level. He based this on HOLMAN's (1996) statistical analysis which concluded that genus/family/order curves of diversity could be real (genetic) or an artefact (taxonomic). KERR (2001) has, however, doubted some of BENTON's data source. HOLMAN (op. cit.) suggested that a real signal could be obtained by the use of monophyletic groups (as in cladistics) and supporting morphological data although GRANTHAM (2001) considered that some paraphyletic taxa are real. In this connection it may be noted that the great majority (90%) of insect orders used in Fig. 8 are considered to be monophyletic (Table I). In addition, mouthpart class data for insects shows a logistic pattern (Fig. 9) providing supporting morphological data. This is, however, not easily reconciled with a phyletic approach to palaeodiversity (ALEKSEEV et al. 2001).

The testing of congruence between phylogeny and the fossil record is at an early stage (WILLS 2001). Interestingly, Atelocerata (Myriapoda + Hexapoda) is more congruent than an (Insecta + Crustacea) clade advocated more recently (DEUVE 2001).

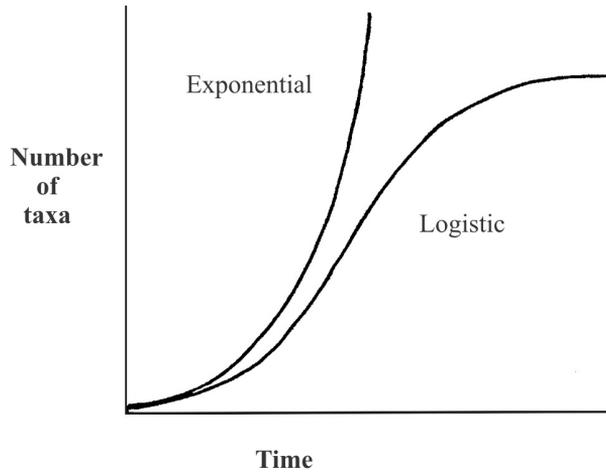


Fig. 5. Ideal curves for exponential (unlimited) and logistic (sigmoidal/constrained) growth.

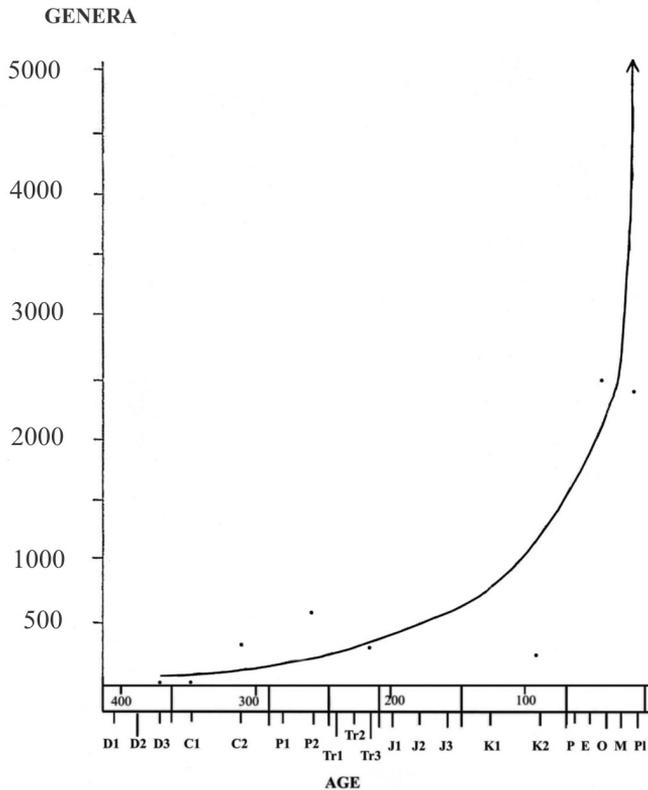


Fig. 6. Cumulative curve for insect generic diversity from Devonian to Recent. Points are totals by period (black circles) and subperiod (open circles). Abbreviations: P1 – Pliocene; M – Miocene; O – Oligocene; E – Eocene; P – Palaeocene; K – Cretaceous; J – Jurassic; Tr – Triassic; P – Permian; C – Carboniferous; D – Devonian; 1, 2, 3, Lower, Middle, Upper. No.s, Ma. Data in JARZEMBOWSKI & ROSS (1996).

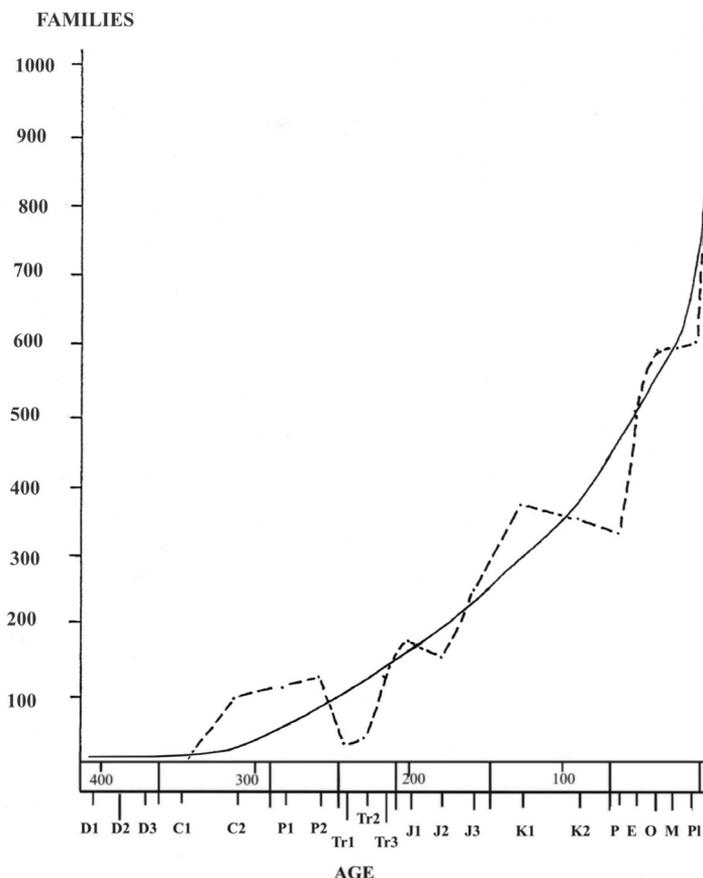


Fig. 7. Cumulative curve for insect family diversity. Explanation as in Fig. 6 except points joined by dashed line.

III. HYPERDIVERSITY

According to HOLMAN (1996) non-insectan higher taxa include an average of 6-12 lower taxa. In contrast, insect orders contain an average of 30-40 families. The 32 extant orders of insects total 967 families (NAUMANN 1995). Families are therefore the number of insect orders nearly to the power two ($32^2 = 1,024$). The 42 extant plus extinct orders (including the unnatural order Protorthoptera) contain over 1,275 families (ROSS et al. 2000). Nearly 70 percent of extant families are known as fossils (JARZEMBOWSKI 2001a) suggesting that at least another 290 families remain to be found. This would give a total of 1,565 families for the Phanerozoic, or nearly the total of natural orders to the power two ($41^2 = 1,681$). Interestingly, insect orders to the power four is 2.8 million, approximately the lower estimate of insect species biodiversity (some 3 million species; BENTON 2001). Insects may be justifiably referred to as hyperdiverse (MAY 1995)! If the effect of the Triassic extinction is ignored by extrapolating from the Permian to Recent, then Phanerozoic ordinal diversity could level off at about 31 orders (Fig. 8). This is close to the number of extant insect orders (32) and, curiously, the number of phyla (31, NIELSEN 1995).

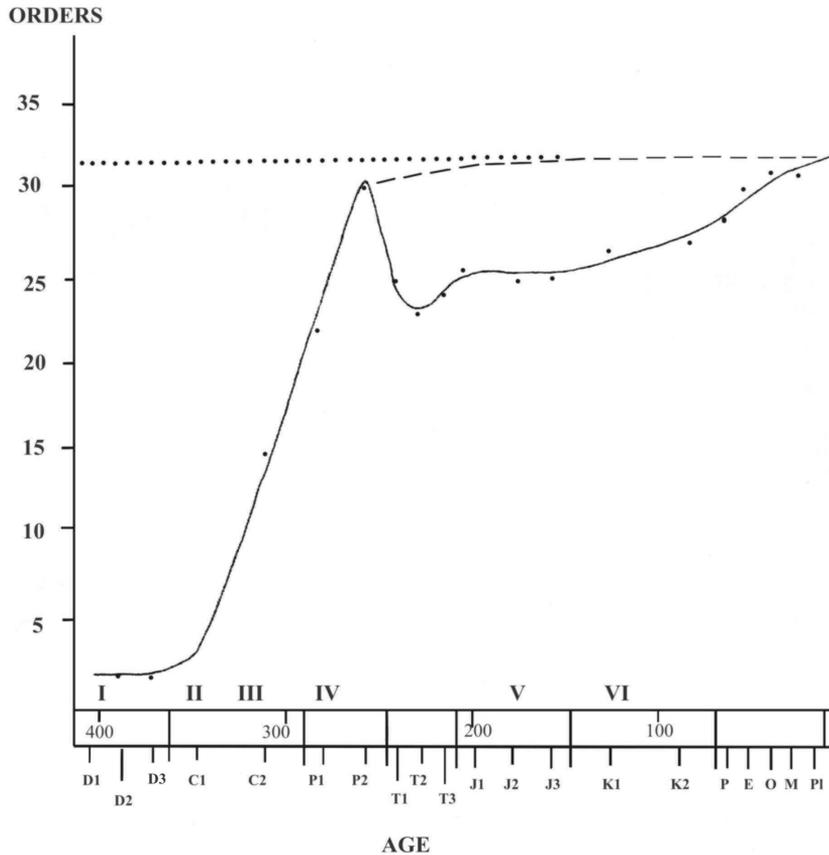


Fig. 8. Cumulative curve for insect orders. Permian – Recent extrapolation, dashed line; ‘K’ value, dotted line. Roman numerals indicate key events (see text). Orders in Tab. I. Other explanation as in Figs 6, 7.

IV. KEY EVENTS

These are indicated by roman numerals in Fig. 8 and summarised below:

- I – earliest hexapods (insects *sensu lato*);
- II – earliest true insects (*Zygentoma* + *Pterygota*); earliest flying insects (*Pterygota*);
- III – near-modern range of plant-feeding strategies in insects;
- IV – radiation of insects with complete metamorphosis (*Holometabola*);
- V – earliest insectan parasites (*Diptera*);
- VI – earliest amberized insects; earliest definite social insects (*Isoptera*).

C o m m e n t s: the hexapod radiation beginning in the Carboniferous seems to have been an adaptive one as opposed to mere contingency because it entailed significant cladogenesis (Table I, Fig. 10). The Carboniferous radiation of the pterygotes effected *Paleoptera* and *Polyneoptera*, whereas the Permian one effected *Paraneoptera* and *Oligoneoptera* (transposed in JARZEMBOWSKI 2001a). The modern predominance of the *Oligoneoptera* (*Holometabola*; Fig. 11) is not evident in the Palaeozoic fauna: (JARZEMBOWSKI & ROSS 1996).

MOUTHPART CLASSES

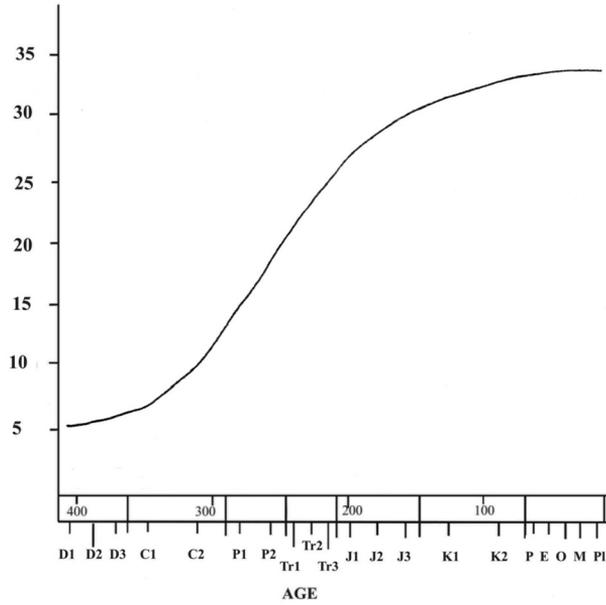


Fig. 9. Cumulative curve for insect mouthpart classes based on data in LABANDEIRA (in press).

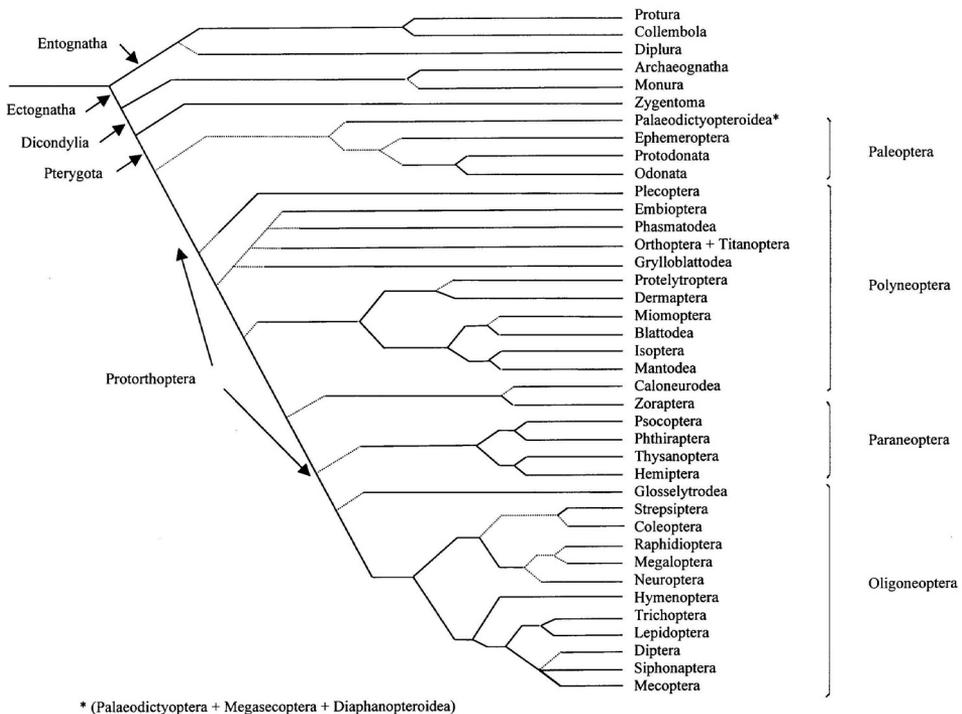


Fig. 10. Provisional relationships among the major hexapod groups. Based on JARZEMBOWSKI (in press).

Table II

Insect orders and the Triassic extinction

Winners

(Orders originating post-Tr2)

1. Protura SILVESTRI, 1907
 20. Dermaptera DE GEER, 1773
 23. Isoptera BRULLÉ, 1832 **
 24. Mantodea BURMEISTER, 1838
 26. Zoraptera SILVESTRI, 1913
 28. Phthiraptera HAECKEL, 1896 *
 32. Strepsiptera KIRBY, 1815 *
 37. Hymenoptera LINNÉ, 1758 ***
 39. Lepidoptera LINNÉ, 1758
 41. Siphonaptera LATREILLE, 1825 * Total 10 orders
- * parasitic ** social *** both in part

Losers

(Palaeozoic orders becoming extinct before Tr2)

5. Monura SHAROV, 1951
7. Palaeodictyoptera GOLDENBERG, 1877
8. Megasecoptera BRONGNIART, 1885
9. Diaphanopteroidea HANDLIRSCH, 1919
19. Protelytroptera TILLYARD, 1931
25. Caloneuroidea HANDLIRSCH, 1937 Total 6 orders

Survivors

(Palaeozoic orders continuing after Tr2)

2. Collembola LUBBOCK, 1871
3. Diplura BÖRNER, 1904
4. Archaeognatha BÖRNER, 1904 ?
6. Zygentoma BÖRNER, 1904
10. Ephemeroptera HYATT & ARMS, 1890
11. Protodonata BRONGNIART, 1893!
12. Odonata FABRICIUS, 1793
13. 'Protorthoptera' HANDLIRSCH, 1906 ?
14. Plecoptera BURMEISTER, 1838
15. Embioptera SHIPLEY, 1904
16. Phasmatodea BRUNNER, 1893
- 17a. Orthoptera OLIVIER, 1789
18. Grylloblattodea BRUES & MELANDER, 1915
21. Miomoptera MARTYNOV, 1927
22. Blattodea BRUNNER, 1882
27. Psocoptera SHIPLEY, 1904
29. Thysanoptera HALIDAY, 1836
30. Hemiptera LINNÉ, 1758
31. Glosselytrodea MARTYNOV, 1938
33. Coleoptera LINNÉ, 1758
34. Raphidioptera LATREILLE, 1810
35. Megaloptera LATREILLE, 1802
36. Neuroptera LINNÉ, 1758
38. Trichoptera KIRBY, 1815
42. Mecoptera PACKARD, 1886 Total 23-25 orders

Specials

- 17b. Titanoptera SHAROV, 1968 (Tr only)
 40. Diptera LINNÉ, 1758 (Originating during Tr extinction)
- Total 2 orders

Approximate Biodiversity of Major Insect Groupings

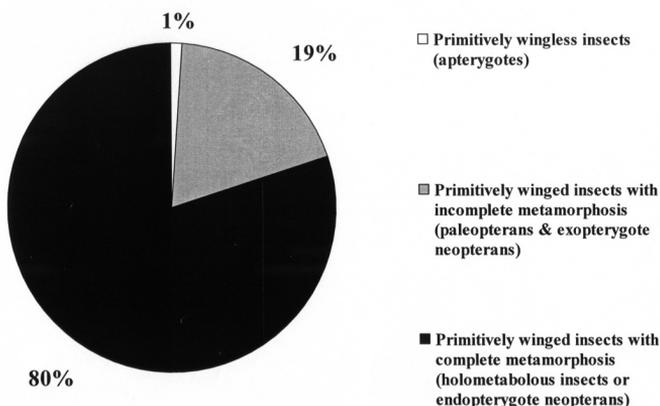
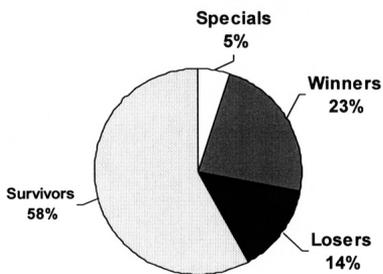


Fig. 11. Recent biodiversity of major hexapod groups (approximate).

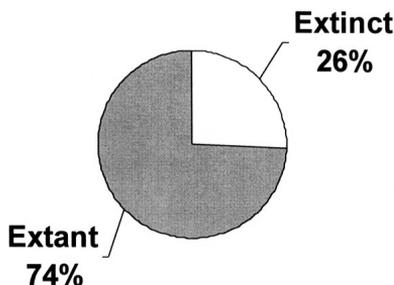
Insect Orders

Triassic Extinction



□ Specials ■ Winners ■ Losers □ Survivors

Phanerozoic Composition



□ Extinct ■ Extant

Fig. 12. Insect orders and the Triassic extinction (left, see Table II); Phanerozoic composition (right, cf. Fig. 4).

Gigantism in fossil arthropods has been linked with high oxygen in the Carboniferous atmosphere predicted by geophysics (DUDLEY 1998). Curiously, the true giants (e.g. protodonate insects, arthropleurid millipedes) are actually less than one percent of all terrestrial arthropods found (personal tally, southern English coalfields). Charcoal is also uncommon and less evident than in some younger non-marine insect-bearing deposits, e.g. the English Wealden. The Carboniferous giant niche seems somewhat vacant on at least a regional scale and combustion elusive as a major environmental stress.

High level changes in Permo-Triassic insects are summarized in Fig. 12 and Table II. The dynamics of change at the Permo-Triassic boundary are still being investigated. However, the change in hemipteran family composition, an important plant-feeding group, seems more abrupt than the changes at either the Jurassic-Cretaceous or Cretaceous-Tertiary boundaries (SHCHERBAKOV 2000). Post-extinction recovery was certainly under way by the Upper Trias (ANDERSON et al. 1998; JARZEMBOWSKI & ROSS 1996). The change at the Cretaceous-Tertiary boundary is now often seen as a low taxonomic one (species level) which is hard to analyse at present in the absence of a suitable insect database (but see MITCHELL, this volume). FARRELL (1998) recognized a post-Cretaceous diversification of plant-feeding beetles (Coleoptera) after the initial radiation of the angiospermous flowering plants. This provides independent support for coevolutionary delay (JARZEMBOWSKI & ROSS 1996). Some workers still regard the Cretaceous record as poor. This is in spite of there being 123 Cretaceous insect localities recognized, compared with 183 Tertiary ones (where the record is considered to be comparatively good) as long ago as ZHERIKHIN (1980). The localities are often of basin size!

V. CONCLUSION

There are still many challenging questions in palaeoentomology and the evolution of insects at the beginning of the twenty-first century. The fossil record needs to be analysed as well as described using mathematics as well as qualitative models. I have tentatively suggested that the Phanerozoic history of insects may be summarised as a logistic curve at bauplan (ordinal) level, offset by historical contingency, notably extinction at the start of the Mesozoic. An exponential model seems more appropriate at lower (family/genus) level. This is hopefully more informative than a straight linear curve at describing Phanerozoic diversity (cf. JARZEMBOWSKI & ROSS 1996). Future work will decide the appropriateness or otherwise of such modelling. How we sample and access the fossil record still poses some special problems, not least discovering the interconnection of species which maintain ecosystems. More work is needed on the ecological implications of abiotic factors like past atmospheric change.

REFERENCES

- ALEKSEEV A. S., DMITRIEV V. Yu., PONOMARENKO A. G. 2001. Evolution of taxonomic diversity. *Ecosystem Restructuring and the Evolution of the Biosphere*, 5, 126 pp.
- ANDERSON J. M., KOHRING R., SCHLÜTER T. 1998. Was insect biodiversity in the Triassic akin to today? – a case study from the Molteno Formation (South Africa). *Entomologia Generalis*, **23**(1/2): 15-26.
- BENTON M. J. (ed.) 1993. The fossil record 2. xvii + 845 pp. CHAPMAN & HALL, London.
- BENTON M. J. 2001. Biodiversity through time. [In:] D. E. G. BRIGGS, P. R. CROWTHER (eds) – Palaeobiology II, 211-220. Blackwell, Oxford.
- BENTON M. J., HARPER D. A. 2000. History of biodiversity. *Geoscientist*, **10**(3): 6-7.
- BENTON M. J., WILLS M. A., HITCHIN R. 2000. Quality of the fossil record through time. *Nature*, **403**: 534-537.
- CRANBROOK EARL OF. 1996. The scientific value of collections. *Sarawak Museum Journal*, **50**(71): 73-86.
- DEUVE T. (ed.) 2001. Origin of the Hexapoda. *Annales de la Société Entomologique de France*, N.S. **37**(1/2): 1-304.
- DUDLEY R. 1998. Atmospheric oxygen, giant Paleozoic insects and the evolution of aerial locomotor performance. *Journal of Experimental Biology*, **201**(8): 1043-1050.
- DUNCAN I. J. 1997. The taphonomy of insects. xvi + 324 pp. Unpublished PhD thesis, University of Bristol.
- FARRELL B. D. 1998. "Inordinate fondness" explained: why are there so many beetles? *Science*, **281**: 555-559.
- GRANTHAM T. 2001. The reality and biological significance of paraphyletic taxa: a philosophical analysis, <http://pjw3.fmnh.org/SepkoskiSymposium/Grantham.html>
- HOLMAN E. W. 1996. The independent variable in the early origin of higher taxa. *Journal of Theoretical Biology*, **181**: 85-94.
- JARZEMBOWSKI E. A. 2001. Palaeodiversity: equilibrium or exponential growth? *Geoscientist*, **11**(4): 12.

- JARZEMBOWSKI E. A. 2001a. The Phanerozoic record of insects. *Acta Geologica Leopoldensia*, **24**(52/53): 73-79.
- JARZEMBOWSKI E. A. In press. *Insecta*. [In:] Encyclopaedia of Life Sciences. Macmillan.
- JARZEMBOWSKI E. A., ROSS A. 1993. The geological record of insects. *Geology Today*, **9**(6): 218-223.
- JARZEMBOWSKI E. A., ROSS A. J. 1996. Insect origination and extinction in the Phanerozoic. [In:] Biotic recovery from mass extinction events. *Geological Society. Special Publication*, **102**: 65-78.
- KERR R. A. 2001. Putting limits on the diversity of life. *Science*, **292**: 1481 [only].
- LABANDEIRA C. C. In press. The history of associations between plants and animals. [In:] C. HERRERA, O. PELLMYR (eds) – History of plant-animal interactions. Blackwell, Oxford.
- MAY R. M. 1995. Conceptual aspects of the quantification of the extent of biological diversity. [In:] D. L. HAWKSWORTH (ed.) – Biodiversity measurement and estimation. CHAPMAN & HALL/Royal Society, London. Pp. 13-20.
- NAUMANN I. D. (ed.) 1994. Systematic and applied entomology. vii + 484 pp., 16 pls. Melbourne University Press, Carlton.
- NIELSEN C. 1995. Animal evolution: interrelationships of the living phyla. 467 pp. Oxford University Press.
- ROSS A. J., JARZEMBOWSKI E. A., BROOKS S. J. 2000. The Cretaceous and Cenozoic record of insects (Hexapoda) with regard to global change. [In:] S. J. CULVER, P. F. RAWSON (eds) – Biotic response to global change: the last 145 million years, Natural History Museum & Cambridge University Press. Pp. 288-302.
- SHCHERBAKOV D. E. 2000. Permian faunas of Homoptera (Hemiptera) in relation to phytogeography and the Permo-Triassic crisis. *Paleontological Journal*, **34**(Supplement 3): 251-267.
- WILLMANN R. 1997. Phylogeny and consequences of phylogenetic systematics. [In:] P. LANDOLT, M. SARTORI (eds) – Ephemeroptera & Plecoptera: Biology – Ecology – Systematics, MTL, Fribourg. Pp. 499-510.
- WILLS M. A. 2001. How good is the fossil record of arthropods? An assessment using the stratigraphic congruence of cladograms. *Geological Journal*, **36**: 187-210.
- WILSON E. O. 1992. The diversity of life. 424 pp., 16 pls. Harvard University Press, Cambridge (Massachusetts).
- ZHERIKHIN V. V. 1980. Nasekomye v ekosistemakh sushi. *Trudy Paleontologicheskogo Instituta*, **175**: 189-224.