Body size and diversity exemplified by three trilobite clades

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Cope's rule concerns only the radiation phase of a clade, overlooking the phase of the clade decline; thus it is incomplete. Changes of body size during the entire evolutionary history of a clade are exemplified here by three trilobite groups – Ptychopariina, Asaphina and Phacopida. Increasing diversity of the clade is associated with increase in maximum body size during the radiation phase, and decreasing diversity is generally associated with a decrease in maximum body size. Two basic patterns of the maximum body size changes are observed during the decline of the clade. The first one is characterized by a high correlation between diversity and the maximum body size, and indicative of species attrition that is nonselective with respect to the body size. The second one is characterized by a weak correlation between diversity and maximum body size, and typical of selective species attrition in relation to size.

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Introduction

The evolutionary history of an extinct clade consists of at least two phases: the phase of diversification or radiation (when species number increase) and the phase of its decline or reduction (when the number of species drop). Cope's rule, an old (Cope 1887) but recently modernized (Stanley 1973) generalization, claims that most groups have evolved from small towards larger body size. This rule concerns only the first, diversification phase of a clade's history (Stanley 1973: figs 5–7). In effect, our knowledge of body size evolution is biased and incomplete as it disregards the evolution of body size during the second phase, when a clade was on the wane. The aim of the present contribution is to present an analysis of changes in body size during the complete evolutionary history of a clade.
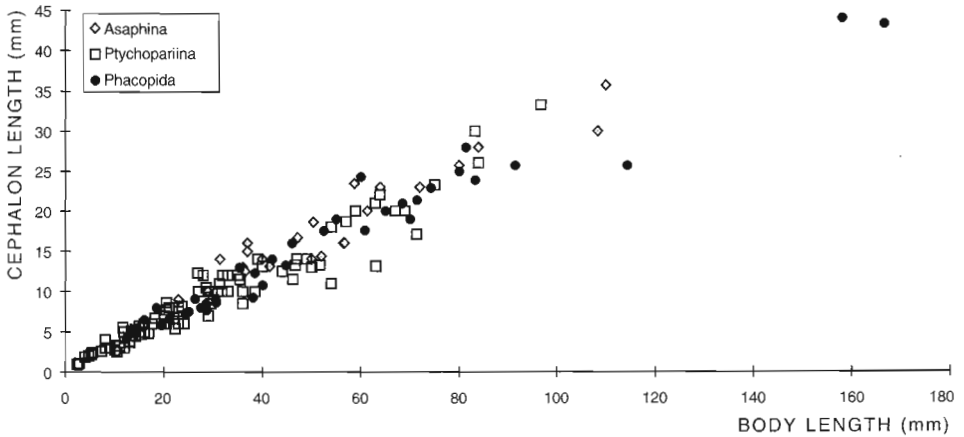
Fig. 1. Body length related to cephalon length in Ptychopariina, Asaphina and Phacopida. Since body length and cephalon length are strongly correlated, length of cephalon can be used as a size-index. Data measured from Harrington *et al.* (1959).

The problem will be exemplified by three trilobite groups: the Early Cambrian–Late Ordovician suborder Ptychopariina Richter, 1933; the Early Cambrian–earliest Silurian suborder Asaphina Salter, 1863; and by the Late Cambrian to Late Devonian order Phacopida Salter, 1864. Body size for individual species was measured on all adult specimens of the aforementioned taxa illustrated in the *Treatise on Invertebrate Paleontology* (Harrington *et al.* 1959). Such data have been proven by our analysis to be statistically representative. Since in most cases the illustrations in the *Treatise* show only cephalons, we measured cephalons' lengths as a proxy for body size. We found that cephalon length is well correlated with the whole body length (Fig. 1) and thus may be used as a size-index. Finally, we constructed size-frequency histograms for various stages of the evolutionary history for each trilobite group studied.

We are aware that since 1959, when the trilobite volume of *Treatise* was published, a large number of new trilobite taxa has been described. We decided, however, to conduct this study on the basis of knowledge of trilobite history recorded until 1959, which, incomplete as it is, demonstrates trends in trilobite evolution. The histogram relating trilobite species number to their body size (Fig. 8) is typical also for other animal taxa (compare May 1988: figs 2 and 6; Jablonsky 1996: fig. 10). This validates the representativeness of the *Treatise* data. It would be interesting to see if data from a larger sample – such as the future edition of the *Treatise* – will confirm our conclusions based on the limited subset.

Results

In the Ptychopariina, the phase of diversification continued from the Early to Late Cambrian, and the phase of reduction from the Late Cambrian to Late Ordovician (Figs 2, 3). In the Asaphina, the phase of diversification persisted from the Middle Cambrian to Early Ordovician, and the phase of reduction from the Early to Late
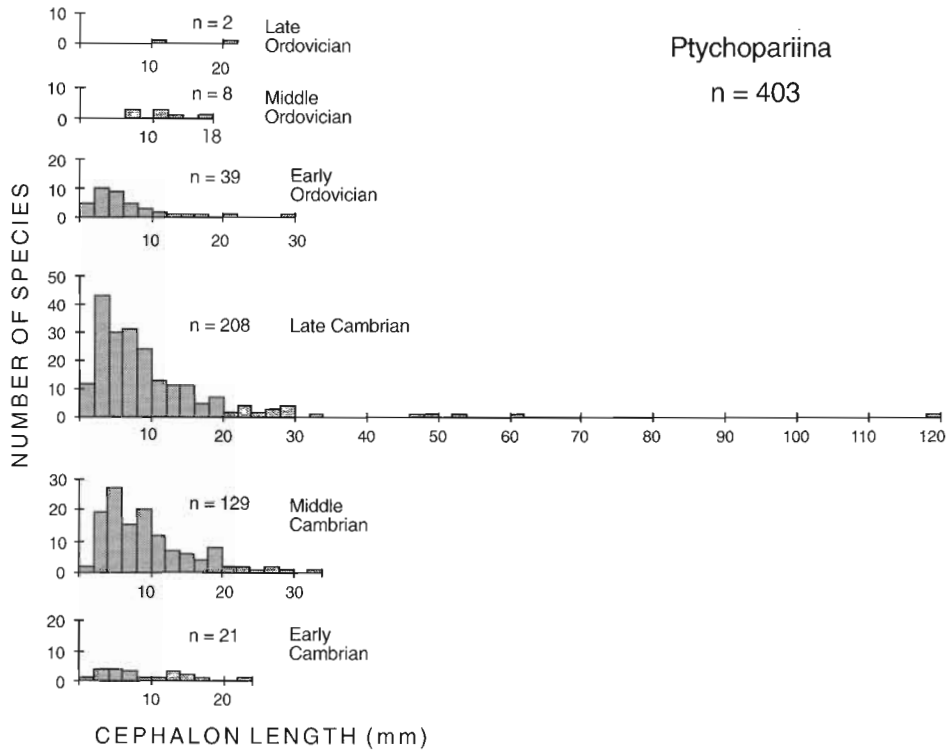
Fig. 2. Frequency distribution of cephalon length among species of Ptychopariina in various intervals of their evolutionary history. During the Cambrian radiation phase, maximum body size and diversity increased, while during Ordovician reduction phase the maximum body size and diversity decreased. Data (including stratigraphic range of the clade) from Harrington *et al.* (1959).

Ordovician (Figs 4, 5). We found that in both groups, maximum cephalon size is strongly correlated with diversity. It increased during the radiation phase, and decreased during the reduction phase (Figs 2–5). To the contrary, we did not find strong correlation between maximum cephalon size and species number in the Phacopida (Figs 6, 7).

Discussion

Many more trilobite species had small and intermediate cephalon sizes than large sizes (Fig. 8). Such a body size pattern is largely result of cladogenetic diffusion (passive trend of McShea 1994) away from an originally small-sized ancestor as shown by Gould (1988) and McKinney (1990a, b). The process of diffusion and, in addition, the higher total origination rate of smaller-sized species then large ones (Dial & Marzluff 1988; McKinney 1990b) implies that the origin of a large trilobite species was a rare or improbable event. Thus the correlation between maximum body size and diversity may be discussed and explained in terms of probability.
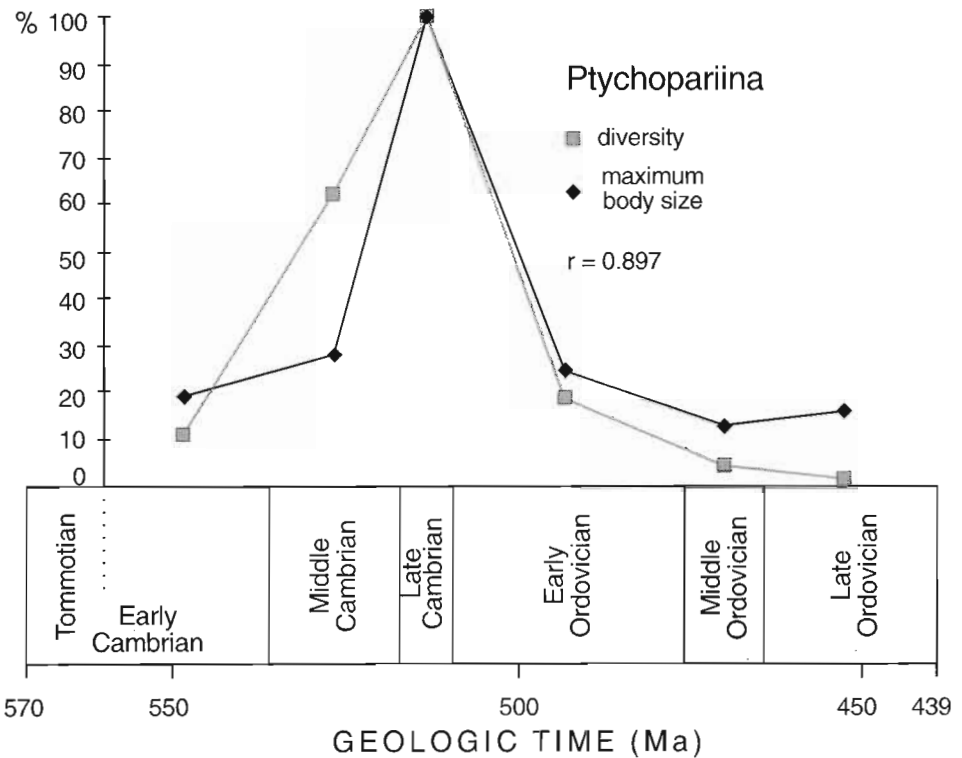
Fig. 3. Changes in the maximum body size and diversity in Ptychopariina plotted as a percentage of maximum; note the very strong correlation ($r = 0.897$). Data from Fig. 2. Time scale after Harland *et al.* (1990).

The radiation phase. — If the probability of the origin of a given species is p, then the origin of this species needs $1/p$ speciations on average. If among 1000 species, only 10 are 50 mm long, then the probability p of origin of species with representatives 50 mm long equals 10/1000 or 0.01. On the other hand, the number of speciations $1/p$ necessary for the origin of species with members 50 mm long equals 1/0.01 or 100. One may use the empirical data (Fig. 8) to estimate the probability of species' origin. Generally, first of all through the work of the cladogenetic diffusion, the larger the body size of a trilobite species, the smaller is the probability p of its origin (Fig. 8), and, consequently, the larger is the number $1/p$ of speciations necessary for its origin. It follows from the fact that when p decreases then $1/p$ increases. This is why maximum body size among trilobites increases with increasing species number (Figs 2–5). This rule is valid not only for trilobites but also for foraminiferans, brachiopods, ammonites, horses, proboscideans, cetaceans, pelycosaurs and rodents (Stanley 1973: figs 5–7; MacFadden 1986; Gould 1988; McKinney 1990b). Furthermore, Müller (1961, 1963, p. 202) noted that the occurrence of gigantic forms among foraminiferans, nautiloids, ammonites, brachiopods and reptiles usually coincided in time with periods of high diversity. Other examples of correlation between large body size and high diversity are mammals and bivalves. Stanley (1979) noted that mammals achieved large size very
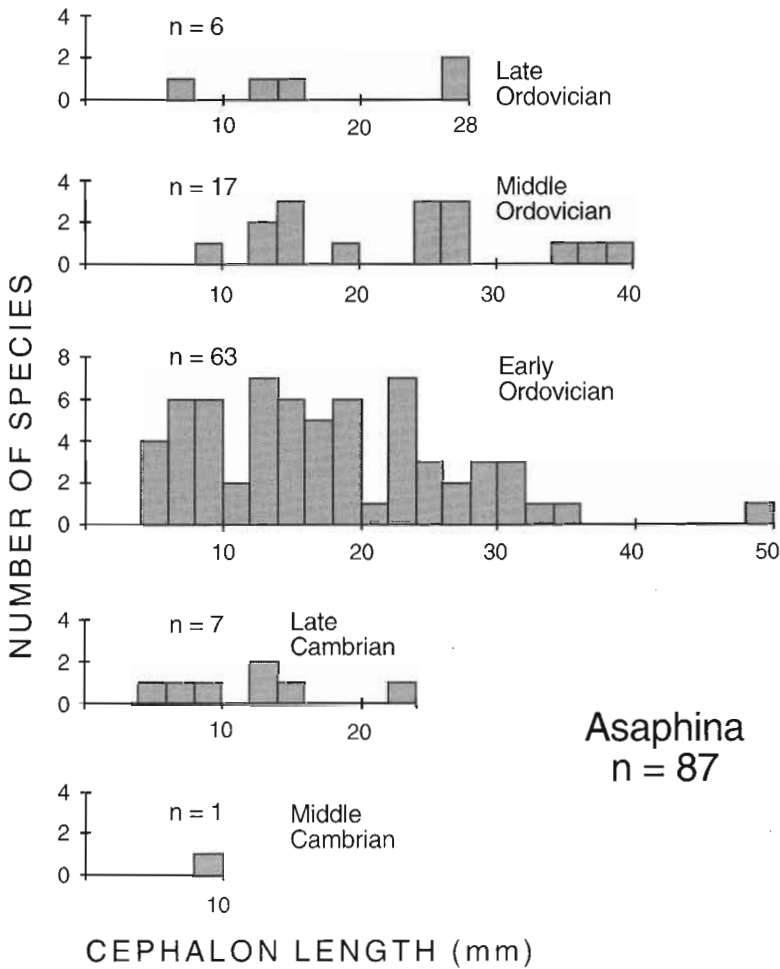
Fig. 4. Frequency distribution of cephalon length among species of Asaphina in various intervals of their evolutionary history. During the Cambrian–Early Ordovician diversification phase, the maximum body size and diversity increased, while during the Ordovician phase of the reduction, maximum body size and diversity decreased. Data (including stratigraphic range of the clade) from Harrington *et al.* (1959).

rapidly, during only in about 10 to 15 Ma of radiation. Bivalves, in contrast, needed much more time to develop large-sized forms. This conforms with our explanation of the phenomenon since mammals' diversification rates were much higher than diversification rates of bivalves (Stanley 1979) so that mammals achieved high diversity much faster.

The reduction phase. — To explain why maximum body size decreases along with decreasing diversity during the reduction phase, two hypotheses can be suggested: a deterministic one and a stochastic null hypothesis. The deterministic hypothesis assumes elevated extinction and/or reduced origination rates of large-bodied trilobite species in comparison with small-sized ones, as postulated by Stanley (1979) and Vrba
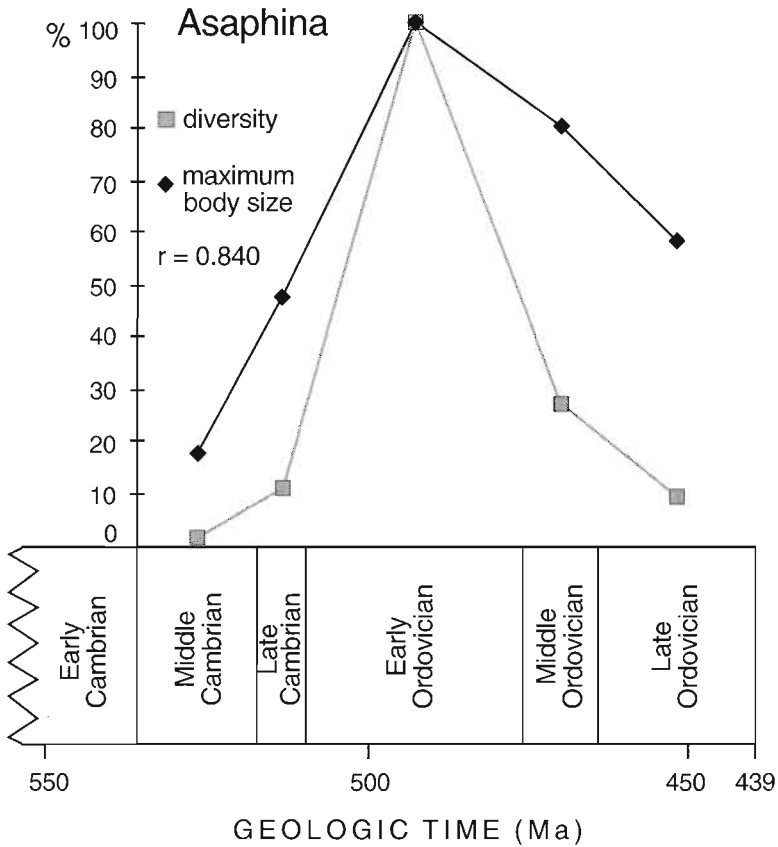
Fig. 5. Changes of the maximum body size compared to changes of the diversity in Asaphina, plotted as a percentage of maximum. Note the strong correlation between size and diversity (*r* = 0.840). Data from Fig. 4. Time scale after Harland *et al.* (1990).

(1983) for all large species. But the assumption mentioned above is not necessary to explain the pattern visible in Figs 2–5. The null hypothesis, on the other hand, assumes that the taxonomic attrition of species during the reduction phase is nonselective with respect to species' body size. For successive time periods, it assumes equal extinction probability q for all species present, no matter if small, intermediate or large (for the positive test see Appendix). To make the problem simpler, the hypothesis omits the influence of species origination because during the reduction phase the rate of extinction greatly exceeds the rate of speciation (compare Harrington *et al.* 1959; Foote 1988). An equal extinction probability for all the species does not mean an equal total probability of extinction for all body sizes present, because individual body size classes are not equally numerous at the beginning of the reduction phase (see e.g., size-frequency histogram for the Late Cambrian in Fig. 2). Large-bodied trilobite species are rare; in general, the smaller are trilobite species, the more frequent they are (Figs 2, 4 and 8). For example, only one Late Cambrian Ptychopariina species falls into the cephalon size class of 118–120 mm, but over 40 species fall into the size class of 2–4 mm (Fig. 2). If one species from the size class 118–120 mm became extinct, the
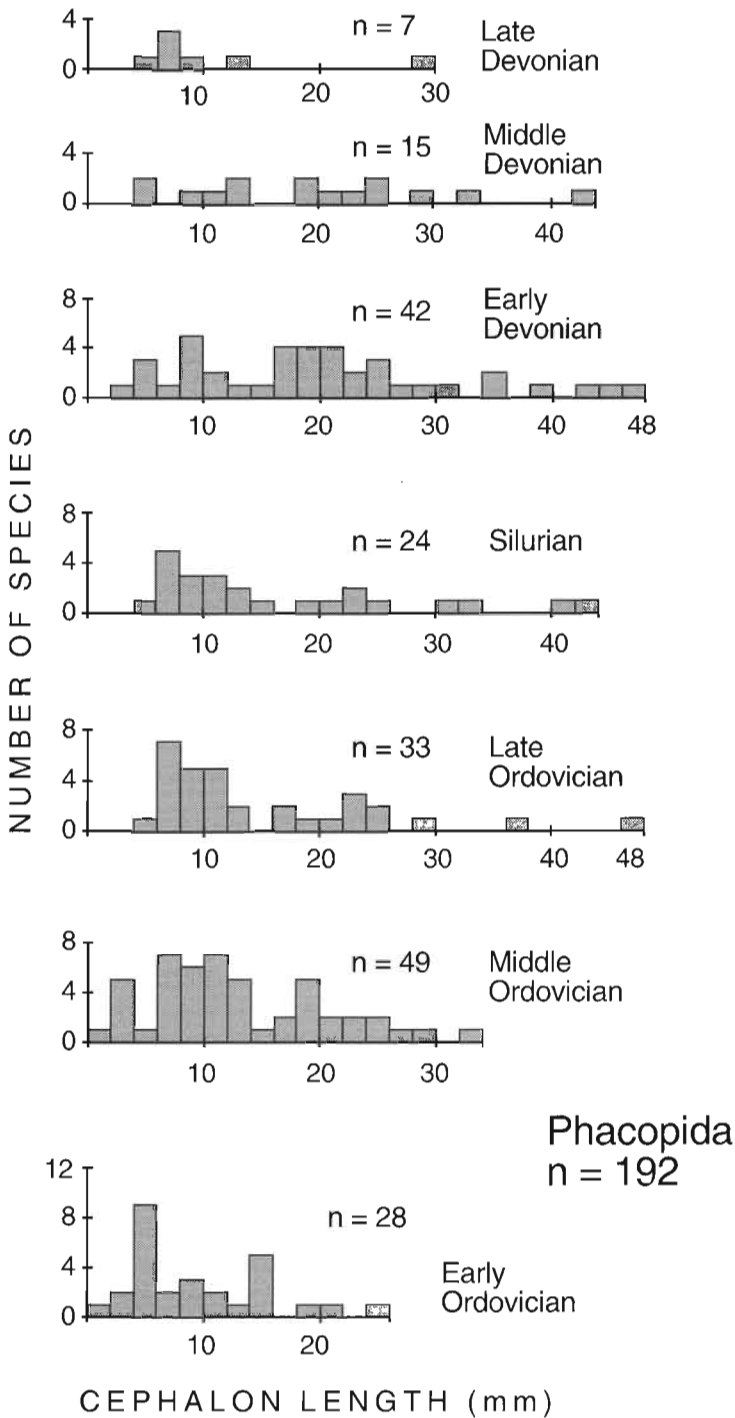
Fig. 6. Frequency distribution of cephalon length of Phacopida species in various intervals of their evolutionary history. Data (including stratigraphic range of the clade) from Harrington *et. al.* (1959).
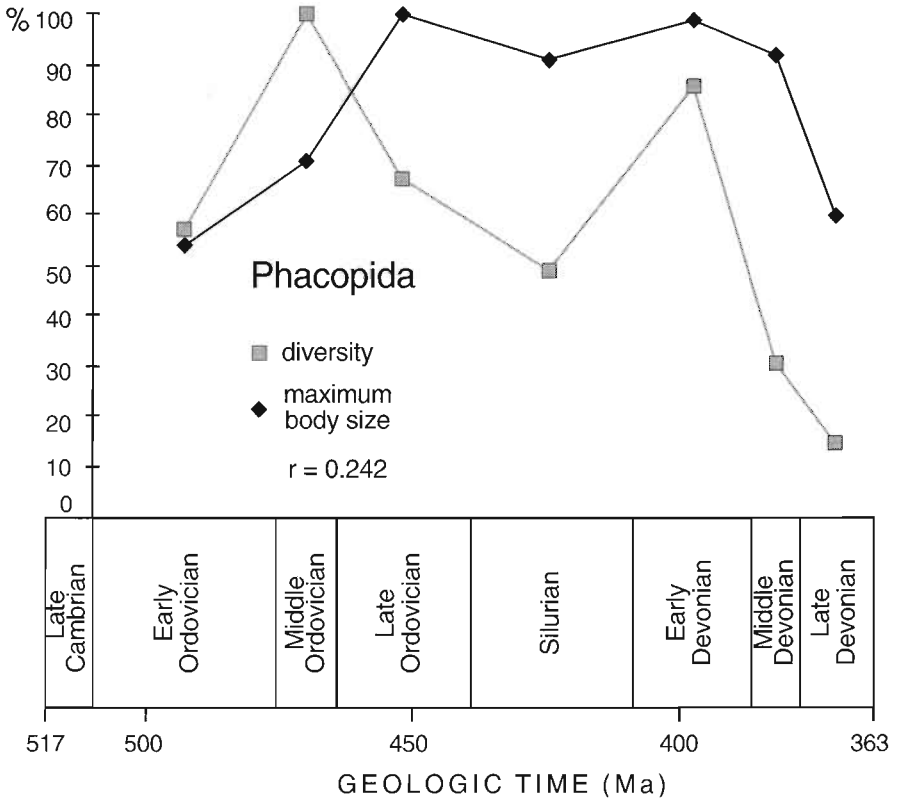
Fig. 7. Changes of maximum body size compared to changes of diversity in Phacopida. Note the weak correlation between size and diversity ($r = 0.242$). Data from Fig. 6. Time scale after Harland *et al.* (1990).

whole size class would vanish. But even if 35 species from the size class 2–4 mm became extinct, this class would continue.

In accordance with the laws of probability concerning compound events, when extinction probability of each species is q, then the probability of simultaneous extinction of two species is q^2, the probability of simultaneous extinction of three species equals q^3 and the probability of extinction of n species equals q^n. The more species-rich a group of species, the smaller is the probability of its complete extinction. Since classes of small body size are species-rich and classes of large body size are very poor in species, classes of large-bodied species are characterized by a higher total probability of extinction in comparison with the classes of small-bodied species, despite the fact that the loss of species diversity is nonselective with respect to body size. During the waning of a clade, large species become extinct faster than small ones (Figs 2, 4), not because they are larger but because they are less numerous (compare McKinney 1990b: p. 107, fig. 4.10; Jablonsky 1996: p. 277). Attrition of a clade during its decline will tend to cause gradual extinction of size classes in order of their increasing species richness (that means classes including smaller and smaller species). In effect, the maximum body size decreases along with decreasing diversity during the reduction phase of a clade's history (Figs 2–5).
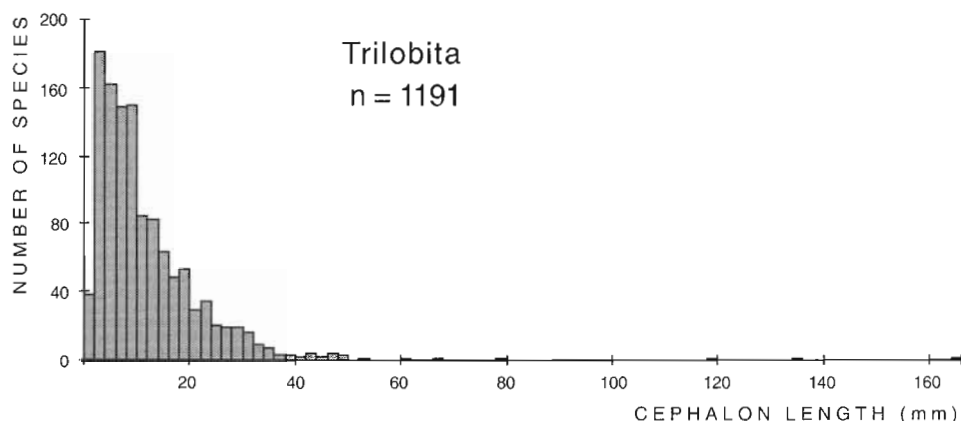
Fig. 8. Distribution of body size in species of Trilobita. Length of the cephalon is used as the size-index. The peak on the side of small sizes results from much higher speciation rate of the smaller species. Data measured from Harrington *et al.* (1959).

We prefer this stochastic hypothesis, instead of the deterministic one, as it is the simpler, null hypothesis. Another reason is that it seems to be supported by investigations concerning cranidial shape outline which suggest nonselective species extinction during the decline of the Ptychopariina and Asaphina (Foote 1993).

The lack of evident dependence of maximum body size on diversity in the reduction phase. — As mentioned earlier, the maximum body size and diversity are weakly correlated in Phacopida, so it may happen that although diversity decreases, the maximum body size increases (Figs 6, 7). This strongly suggests a taxonomic attrition that is selective with regard to body size during the reduction phase. In general, elevated origination and/or reduced extinction in regions of morphospace occupied by large-bodied species had to exist, otherwise large-bodied species, which belong to species-poor size classes, should have vanished first when diversity decreased. In particular, the origin of new large-size species in the face of decrease of total diversity resulting from the extinction of smaller species in the Late Ordovician (Fig. 6) has caused the lack of evident dependence of maximum body size on diversity. The data of Foote (1993) also suggest selective species reduction during the decline of Phacopida and seem to support our conclusions in this respect.

Test for presence or absence of selectivity. — As shown above, there are two basic patterns of body size evolution during the reduction phase of a clade. The first one with a high correlation between the diversity and the maximum body size (Figs 3, 5), and the second one that is characterized by weak correlation between these two variables (Fig. 7). The first pattern may serve as an indicator that the clade decline is nonselective with regard to body size, while the second one may indicate a clade reduction selective with respect to size.

Size-diversity relationship of recent taxa. — The analysis of the interdependence of body size and diversity in the fossil record may add a historical perspective to the study of body size patterns of species diversity of Recent taxa. Size-frequency plot for species of a Recent taxon may be compared to a single film frame while time-series

plots for fossil species to a whole film sequence. Rosenzweig (1995: pp. 73–77) presented a summary of knowledge of the body size patterns of the species diversity among Recent groups. Most extant organisms display more numerous intermediate-size species than either very large or very small ones. But there are also groups where small body sizes are most common. Rosenzweig (1995) admits that ecologists cannot explain the size-diversity patterns of Recent taxa. The message from the fossil record (Stanley 1973 and this paper) is that the unimodal size-diversity relationship may appear at the beginning of the diversification phase, and at the termination of the reduction phase of the history of a clade when diversity is relatively low. The positively skewed body size histograms are typical of periods of the acme of a clade when diversity is relatively high. Thus the shape of the body size histogram of a particular Recent taxon may depend on the current phase of the evolutionary history of the clade.

Conclusions

1. Cope's rule did not concern a complete evolutionary history of a clade but only its radiation phase.

2. Cope's rule may be redefined as follows: 'During the radiation phase of a clade, the maximum body size is diversity dependent in such a way that increase in diversity is associated with increasing maximum body size'.

3. The radiation phase is selective with respect to body size because small-bodied species have much higher total speciation rates than large-bodied ones.

4. During the decline of a clade, the maximum body size is in principle diversity dependent such that decrease in diversity is associated with a decreasing maximum body size.

5. There are two basic patterns of maximum body size modifications during the decline of a clade. The first pattern occurs when strong correlation between the diversity and the maximum body size exists, and is indicative of nonselective species attrition. The second pattern occurs when the correlation between diversity and the maximum body size is weak, and is indicative of the attrition which is selective in respect to size.

Acknowledgments

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Zależność między maksymalną wielkością ciała a zróżnicowaniem gatunkowym na przykładzie trzech grup trylobitów
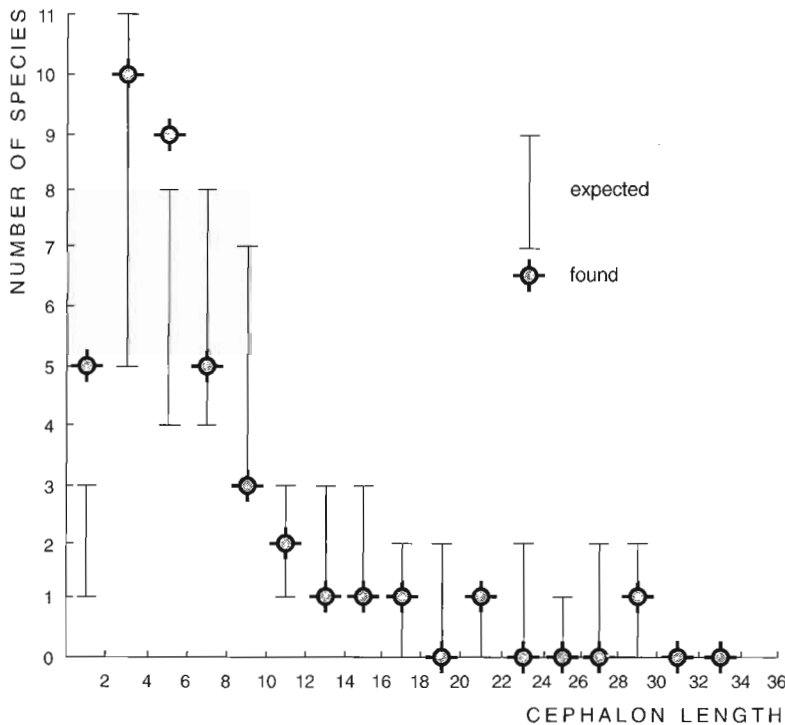
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Streszczenie

Ewolucyjna historia wymarłej grupy składa się przynajmniej z dwu faz: z fazy radiacji – gdy liczba gatunków się zwiększa, oraz fazy redukcji – kiedy liczba gatunków spada. W fazie radiacji, zgodnie z regułą Cope'a, wraz z rosnącą liczbą gatunków, rośnie też na drodze kladogenetycznej dyfuzji (Gould 1988; McKinney 1990a, b) maksymalna wielkość ciała w grupie (Fig. 2–7), tzn. pojawiają się gatunki obejmujące osobniki o coraz to większych rozmiarach ciała. Natomiast w fazie redukcji zachodzi odwrotny proces: zmniejszającej się liczbie gatunków towarzyszy równoczesny spadek maksymalnej wielkości ciała w grupie (Fig. 2–7). Silna korelacja między liczbą gatunków a maksymalną wielkością ciała w czasie redukcji grupy (Fig. 3, 5) wskazuje, że powodujące redukcję wymieranie odbywało się bez selekcji na wielkość. Słaba korelacja między obiema wielkościami (Fig. 7) jest natomiast przejawem istnienia doboru zależnego od rozmiarów ciała w czasie wymierania.

Appendix

Table 1 and Fig. 1. Expected and found species number of Early Ordovician Ptychopariina to test the null hypothesis.

size class (mm)			0–2	2–4	4–6	6–8	8–10	10–12	12–14	14–16	16–18
species number	Late Cambrian (found)		12	43	30	31	24	13	11	11	5
	Early Ordovician	found	5	10	9	5	3	2	1	1	1
		expected	2±1	8±3	6±2	6±2	5±2	2±1	2±1	2±1	1±1

size class (mm)			18–20	20–22	22–24	24–26	26–28	28–30	30–32	32–34
species number	Late Cambrian (found)		7	2	4	2	3	4	0	1
	Early Ordovician	found	0	1	0	0	0	1	0	0
		expected	1±1	0±1	1±1	0±1	1±1	1±1	0	0

Expected species number for each size class was calculated according to the equation:

$$N_2 = N_1 \cdot p \pm \sqrt{N_1 \cdot p \cdot (1-p)}$$

where: N_2 – expected Early Ordovician species number in a given size class, N_1 – Late Cambrian species number found in a given size class, p – probability of species survival ($p = N_{t2}/N_{t1}$), N_{t1} – total found Late Cambrian species number, N_{t2} – total found Early Ordovician species number.