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Some Questions about the Evolution of Life — History traits in Diplopoda

by

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A b s t r a c t : Current modes of variation in life-history traits are reviewed in four orders of Diplopoda by means of interspecific and intraspecific comparisons. The traits taken into account are stadium and age of females at the first oviposition, their fecundity and their mode of reproduction (semelparity or iteroparity). Such questions as these arise: Has the stadium or the age at the first oviposition a genetic basis in Iulida and Blaniulida? Has the relationship between fecundity and number of rings a general significance? Are semelparity and iteroparity variable traits or do they obey phylogenetic constraints? The evolution of life-history traits in Diplopoda is discussed in relation to the answers to these questions, and to the definition of fitness (r or K).

1. Introduction:

Life-history traits are being described in an increasing number of natural populations of Diplopoda, and this paper deals with the stadium and age of females at the first oviposition, their fecundity and their subsequent mode of survival (semelparity or iteroparity).

In the orders Craspedosomatida, Polydesmida, Iulida and Blaniulida[1], current knowledge makes it possible not only to have a comprehensive view of these traits, but also to research their modes of variation by means of intraspecific as well as interspecific comparisons. Most of these modes of variation are still hypothetical and many questions arise about them. However, such data are essential to investigate how life-history traits have evolved in the past. In this paper, an attempt is made with this end in view, assuming two further points in accordance with the neo-Darwinian theory: a) evolution has maximized fitness; b) there is no difference between micro- and macroevolutionary processes.

2. Current Modes of Variation:

2.1. Craspedosomatida, Polydesmida:

In the Craspedosomatida and Polydesmida (Tab. 1), within each species, the number of rings of a given stadium does not change, and, above all, neither does the mature stadium. A phylogenetic constraint links the achievement of maturity to a given stadium. It is also the only one in which oviposition occurs, because females are not capable of surviving and moulting after their first breeding season (semelparity).

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1) The classification after DEMANGE (1981) can be easily transposed into another system. But if one refers to ENGHOFFs (1981) classification in which Blaniulidae and Nemasomatidae are not directly related, it is better to leave out *Nemasoma varicorne* in the parts of this paper dealing with Blaniulida.

Table 1: Oviposition in natural populations of Craspedosomatida and Polydesmida.

Species	Location	Stadium (and podous rings)	Usual Age [years]	References
Craspedosomatida				
Chamaesoma brolemanni RIBAUT et VERHOEFF	France < 200 m	VIII (23)	1	DAVID (1989)
Melogona scutellare (RIBAUT)	GB Wales	VIII (25)	1	BLOWER (1979)
M. scutellare	GB England	VIII (25)	1	ibidem
Melogona gallica (LATZEL)	France < 200 m	IX (27)	1	DAVID (1984)
Chordeuma sylvestre C.L. KOCH	Germany < 400 m	IX (27)	1	DUNGER & STEINMETZGER (1981)
Chordeuma proximum RIBAUT	GB England	IX (27)	1	READ (1988 a)
Nanogona polydesmoides (LEACH)	GB England	IX (27)	1	BLOWER (1985)
Craspedosoma alemannicum VERHOEFF	Germany (diverse)	IX (27)	1	VERHOEFF (1929)
C. alemannicum	Switzerland 1000 m	IX (27)	2	PEDROLI-CHRISTEN (1978)
Xylophageuma zschokkei BIGLER	Switzerland 1000 m	IX (27)	1 or 2	ibidem
Ochogona caroli (ROTHENBÜHLER)	Austria 2000 m	IX (27)	3	MEYER (1979)
Haasea fonticulorum (VERHOEFF)	Austria 2000 m	IX (27)	3	ibidem
Anamastigona matsakisi MAURIES et KARAMAOUNA	Southern Greece	IX (27)	2	KARAMAOUNA (1987)
Polydesmida				
Brachydesmus superus LATZEL	GB Wales	VII (17)	1	BLOWER (1979)
Polydesmus angustus LATZEL	France < 200 m	VIII (18)	1 or 2	COURET (1985)
Polydesmus inconstans LATZEL	USA Michigan 1	VIII (18)	1	SNIDER (1984)
P. inconstans	USA Michigan 2	VIII (18)	1 or 2	ibidem
Polydesmus graecus DADAY	Southern Greece	VIII (18)	2	KARAMAOUNA (1987)
Tymbodesmus falcatus KARSCH	Nigeria, dry season	VIII (18)	2	LEWIS (1971 a)
Habrodesmus duboscqui BROLEMANN	Nigeria, dry season	VIII (18)	1 or 2	LEWIS (1971 b)
Xanthodesmus physkon (ATTEMS)	Nigeria, dry season	VIII (18)	1	ibidem

In both orders, there is interspecific variation in the mature stadium, but comparatively little. In Craspedosomatida, it can be stadium IX with 27 podous rings; or stadium VIII with 25 podous rings (*Melogona scutellare*), i.e. one stadium before the preceding case; or else stadium VIII with 23 podous rings (*Chamaesoma brolemanni*), which corresponds to one apodous ring less in stadia VI and VII. In Polydesmida, the mature stadium can be stadium VIII with 18 podous rings, or stadium VII with 17 podous rings, i.e. one stadium before the preceding case.

There is more variation in the generation time, and two variability levels are known. First, a macroclimatic level which is mainly apparent in the Craspedosomatida. The life-cycle is usually an-

nual in all the populations studied in humid temperate Europe at a low altitude (8 cases), but it lengthens up to 2 years where altitude increases, or under a Mediterranean climate with dry summers; it even reaches 3 years at a very high altitude. Comparing different populations of the same species, it can be seen that the generation time of *Craspedosoma alemannicum* is 1 year in southern Germany and 2 years at an altitude of 1000 m in Switzerland. Moreover, within a usually annual population, a majority of animals can develop in 2 years under exceptional conditions, as happened in a French population of *C. brolemanni* after a severe drought (DAVID 1989). In other words, there is a substantial plasticity of the duration of stadia in relation to climatic conditions, and the question is whether the interspecific variation in the Craspedosomatida is to a great extent determined by this plasticity. In this case, the generation times of species could depend directly on the places where they live. Alternatively, they could be adaptations with a genetic basis.

In the Polydesmida, the macroclimatic level of variability is not very apparent in the natural populations studied so far (generation time is always 1 or 2 years), but no data have been obtained at high altitudes. Still the fact remains that some intraspecific plasticity has been proved experimentally by rearing *Polydesmus inconstans* at several temperatures (SNIDER 1981 a), which can explain some variation from year to year in the generation time of a population, as in Craspedosomatida.

There is a second level of variability in these orders. Within a population, during a given year, one often meets with individuals which take 1 year or 2 years to lay eggs, both parties being numerous in Polydesmida (e. g. *Polydesmus inconstans* in the USA, *P. angustus* in France). As pointed out by SNIDER (1984), this implies that macroclimatic conditions are no longer involved. An extended period of oviposition has been brought forward to account for this phenomenon, and there is no doubt that it plays a role. However, COURET (1985) has shown in *P. angustus* that the individuals of the same nest, kept under the same temperature conditions, have one-year and two-year life-cycles. Considering such a result, the question is whether the factors involved are microclimatic, trophic, genetic, or else a combination of these. And things may be as complicated in the Craspedosomatida.

From an adaptive point of view this second level of variability can be advantageous, particularly if young stadia are very vulnerable, as it spreads the risks of extinction (DEN BOER 1968).

2.2. Iulida, Blaniulida:

Current knowledge leads to a very different picture in the Iulida and Blaniulida.

Firstly, the number of rings of a given stadium may differ within each species and even each population, for genetic or environmental reasons. Secondly, maturation is somewhat independent of growth: within each population, the first oviposition can occur from a given stadium (which will be referred to as the minimum stadium), but it sometimes occurs one or two stadia onwards. Lastly, the interspecific variation in both the stadium and the age of oviposition is considerable, even under the same climatic conditions.

With regard to the Iulida Cylindroiulinae in humid temperate Europe at a low altitude, the life-histories of which are fairly well known in seven populations (Tab. 2), there is a conspicuous relationship between the minimum stadium and the age at females' first oviposition (first is specified because females are iteroparous in all these Cylindroiulinae, breeding in successive years). Species which begin to oviposit in a higher stadium take more time to reach it (Fig. 1), and the relationship still holds if the number of rings is substituted for the stadium. It looks as though the different species in this area have approximately the same growth rate, as far as stadia and numbers of rings are concerned, but begin to oviposit after a more or less extended growth. Such interspecific differences are unlikely to originate from purely environmental factors associated with species' habitats, as has been hypothesized in the Craspedosomatida; they are more likely to have a genetic basis, although this point can be challenged. As a result, the question arises: which of the correlated variables, sta-

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Table 2: First oviposition in natural populations of Iulida and Blaniulida (humid temperate Europe; low or medium altitude): [1] Dots indicate uncertainty about an extra stadium at the first oviposition. S semelparity, I iteroparity.

Species	Location	Stadia[1])	Podous rings	Age (years)	S/I	References
Iulida						
Cylindroiulinae						
Cylindroiulus latestriatus (CURTIS)	Belgium	VII-VIII ...	29-38	2	I	BIERNAUX (1972)
C. latestriatus	GB England	VII-VIII ...	30-38	2	I	BLOWER & GABBUTT (1964)
Cylindroiulus occultus (C.L. KOCH)	Germany	VIII-IX	38-47	3	I	VOIGTLÄNDER (1987)
Enantiulus nanus (LATZEL)	Germany	VIII-IX ...	38-49	3	I	ibidem
Cylindroiulus punctatus (LEACH)	GB England	VIII ...	40-43	3	I	BLOWER & GABBUTT (1964)
Cylindroiulus nitidus (VERHOEFF)	GB England	IX ...	41-45	4	I	BLOWER & MILLER (1977)
C. nitidus	France	X-XI	43-50	4	I	DAVID (1982)
Iulinae						
Ophyiulus pilosus (NEWPORT)	GB Wales	X-XI	48-54	2	S	BLOWER & MILLER (1974)
Iulus scandinavius LATZEL	GB England	X-XI	43-49	3	S	BLOWER (1970)
Blaniulida						
Nemasoma varicorne C.L. KOCH	GB England	VI ...	23-25	2	I	BROOKES (1974)
Proteroiulus fuscus (AM STEIN)	Poland	VII	26-28	3	I	TRACZ (1984)
P. fuscus	GB England	VII-VIII	26-31	3	I	BROOKES (1974)
Blaniulus guttulatus (F.)	GB Wales	IX	36-42	4	I	BROOKES & WILLOUGHBY (1978)

dium and age, is the independent one? Either the minimum stadium has a species-specific genetic basis: as soon as this stadium is reached, or passed, the first oviposition can occur in the next spring; given the growth rate, the age at the first oviposition is just a correlate of this stadium. Or, on the contrary, the age at the first oviposition has a species-specific genetic basis and, given the growth rate, the stadium at the first oviposition is just a correlate of this age.

The comparison of two populations of *Cylindroiulus nitidus* in England and France, where females lay eggs at the same age while differing by one stadium, suggests that the first oviposition of this species may be set at 4 years, and that the stadium depends on the precise growth rate during these years. Small variation in the growth rate may be conditional on individual, year, and more or less favourable local features.

Data on four populations of Blaniulida (1 in the Nemasomatidae and 3 in the Blaniulidae) suggest the same phenomenon (Table 2 and Fig. 1): a) at a rough estimate, there is a growth rate common to several species (lower in the Blaniulida than in the Cylindroiulinae), which gives rise to a relationship between the minimum stadium and the age at females' first oviposition; b) with regard
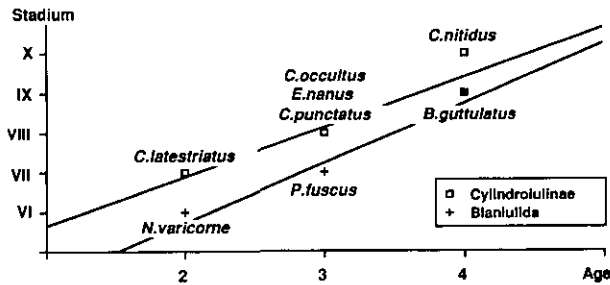
Fig. 1: Linear relations between minimum stadium and age of females at first oviposition in Iulida Cylindroiulinae and Blaniulida.

to *Proteroiulus fuscus*, its age at the first oviposition may be set at 3 years, and eggs are laid in stadium VII in western Poland, but occasionally in stadium VIII in England where climatic conditions are more favourable to growth.

In the Iulida Iulinae the data are more scarce but more complicated, because the different species have very different growth rates. In Great Britain, the same stadia are reached after 2 years in *Ophyiulus pilosus* and 3 years in *Iulus scandinavius*. In that case, no relationship between the stadium and the age at females' oviposition could appear. However, the question above remains. If the age of oviposition had a genetic basis, that could easily account for the variation from year to year in the egg-laying stadium of a population of *I. scandinavius* (BLOWER 1970): stadium X would correspond to a growth in less favourable conditions than stadium XI. Conversely, if the stadium had a genetic basis, that could account for the fact that these closely related Iulinae have the same minimum stadium of oviposition, stadium X; even in another climatic area (in Austria at an altitude of 1900 m), *Leptoiulus saltuvagus* can lay eggs from stadium X with a generation time of at least 4 years (MEYER 1985).

In the opinion of most authors, the stadium of oviposition determines the age, not the reverse. For example, FAIRHURST (1974), owing to the fact that oviposition begins in stadium X, at the age of 3 years, in a Welsh population of *Ommatoiulus sabulosus*, infers that it must take one year more in another population where the oviposition begins in stadium XI. In another example, BROOKES (1974) comparing the life-cycles of *P. fuscus* and *Nemasoma varicorne* in England, writes "by advancing the attainment of maturity by one stadium (*N. varicorne*) eliminates one year from its cycle". Studies would be welcome in order to know whether this interpretation is correct, or whether *N. varicorne* eliminates one stadium from its life-cycle because it breeds one year sooner. This difference is of importance with respect to evolutionary considerations.

2.3. Fecundity in Diplopoda:

Fecundity is certainly a very important life-history trait, but current knowledge of this parameter is somewhat inaccurate in Diplopoda.

In many Iulida, the dissection of females shows that ovocyte maturation advances in a synchronized way during some months. It is therefore possible to estimate fecundity by dissecting ovigerous females at the suitable time (towards the end of maturation, but before the beginning of oviposition). The same holds good for the Polyzoniida, in which it is also possible to collect brooding females in the field. Important results have been obtained in this way, showing that, in a given population, fecundity increases with the number of rings of females (Fig. 2). If this relationship holds true for different populations of a species, or closely related species of a genus, it is of great significance from an evolutionary point of view. Unfortunately, its validity is difficult to prove for different reasons.
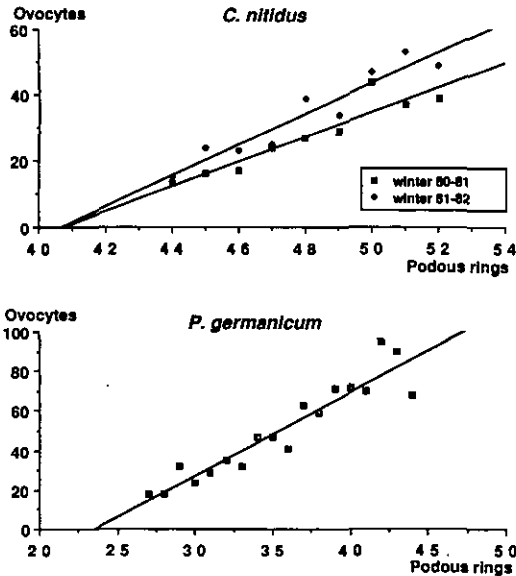
Fig. 2: Linear relations between fecundity and number of podous rings in single populations of
C. nitidus (after DAVID 1982) and P. germanicum (after COURET & DAVID 1985).

On the one hand, other dimensions influence fecundity, such as body width, as shown by
BAKER (1984) in different populations of *Ommatoiulus moreletii.* Body width evolving inde-
pendently of the number of podous rings — cf. ENGHOFF's (1982) analysis of data from an insular
species swarm — a relationship is more likely to exist between fecundity and either volume or bio-
mass. Again, that might be complicated by environmental factors (LEWIS 1971 a).

On the other hand, fecundity is not known accurately in many species which lay their eggs pro-
gressively or repeatedly, notably in some Blaniulida, Craspedosomatida and Polydesmida.
SNIDER (1981 b) has counted on average 10 ovipositions per female in *P. inconstans* kept in the la-
boratory at 15° C, which averages 469 eggs per female during a breeding season; this amount is
much larger than can be estimated by counting the number of eggs per nest, or even by dissecting fe-
males.

The gathering of new biological data in this field is indispensable for understanding how life-
history traits have evolved in Diplopoda.

2.4. Semelparity and Iteroparity:

BLOWER (1969 a) assumed that both these modes of reproduction might be adaptations to
different kinds of resource distribution: iteroparous species would be adapted for dispersal to
widely scattered resources, whereas semelparous ones would utilize evenly spread resources. How-
ever, that hypothesis has been strongly questioned by the fact that *C. nitidus* "does not appear to
face the dispersal hazards instanced ... as a reason for iteroparity" (BLOWER & MILLER 1977).
And many other cases, e. g. *Blaniulus guttulatus* and *Glomeris marginata,* do not confirm such an
adaptive significance of these life-history traits.

Actually, semelparity and iteroparity appear to be closely linked to the taxonomic position of
species: in Tables 1 and 2, all Craspedosomatida, Polydesmida and Iulida Iulinae are semelparous,
whereas all Blaniulida and Iulida Cylindroiulinae are iteroparous. READ (1988 b) regards some

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Madeiran *Cylindroiulus* as possibly semelparous, but this conclusion based on rather limited data is doubtful. Further studies are necessary for knowing whether these life-history traits can vary between closely related species under particular conditions, or if they obey strong phylogenetic constraints.

3. Speculation on Evolutionary Processes:

In order to investigate the evolution of life-history traits, one must assume, as a tool, that evolution maximizes individuals' fitness. However, there are several definitions of fitness which can lead to conflicting conclusions.

3. 1. r as a Measure of Fitness:

In expanding populations — including every population controlled in a density-independent manner — genotypes which confer a maximum rate of population growth are favoured and the intrinsic rate of increase, r, can be a measure of fitness. One way of estimating it, is: $r = Ln\ Ro\ /\ T$. In this formula, Ro is the replacement rate, i. e. the average number of offspring produced by an animal during its life-time, which depends on both the probability of survival up to reproduction(s) and fecundity(ies); T is the mean generation time.

Knowledge of Diplopod population biology is not yet sufficient to calculate r in many species under given conditions, and to allow conclusions to be drawn. But it is worth considering the two evolutionary processes that may maximize r, an increase in Ro and a decrease in T.

a) Increase in Ro. In addition to many morphological, physiological and behavioural adaptations which may improve survival in different stadia, an increase in the replacement rate depends on an increase in fecundity. As mentioned above, that may be closely related to the increase in adult's size in Diplopoda, which can be achieved in several ways:

(i) Higher numbers of rings added at each moult, or larger rings added at each moult. The age and stadium at the first oviposition remaining the same, fecundity is increased without survival being necessarily affected. A "lengthwise evolution" of this type is perhaps occurring at the present time in populations of *Tachypodoiulus niger* living at different altitudes (SAHLI 1969, 1978).

(ii) Faster stadial succession. Provided that the age at the first oviposition has a genetic basis in the Iulida and Blaniulida, mutations improving the growth rate lead to bigger adults in a given time.

(iii) Oviposition delayed up to a bigger stadium and an older age, or oviposition extended over bigger stadia by acquiring iteroparity. Although both these ways of increasing Ro also imply an increase in the generation time, they can be selected if $Ro' > Ro^{(T/T)}$, a condition easier to satisfy when T is high or Ro low (Fig. 3 a).

The relation between r, Ro and T nevertheless limits the increase in Ro, because it ends by showing a very small gain in r, particularly if T is high (Fig. 3).

b) Decrease in T. A decrease in the mean generation time can also be achieved in several ways in Diplopoda:

(i) Faster stadial succession. In species with a given stadium of oviposition (Craspedosomatida, Polydesmida and, possibly, Iulida and Blaniulida if their minimum stadium of oviposition has a genetic basis), mutations improving the growth rate lead to a smaller number of years to achieve maturity. T is decreased without Ro being necessarily affected.

(ii) Oviposition brought forward to a younger age and a smaller stadium. Although it may imply a decrease in Ro, it can be selected if $Ro^{(T/T)} < Ro' < Ro$ (Fig. 3 b). An evolution of this type might have occured in the Cylindroiulinae of temperate Europe, if r is higher in *C. latestriatus* than in *C. punctatus,* and a fortiori *C. nitidus,* as suggested by BLOWER (1969).

(iii) Evolution from iteroparity to semelparity by concentrating all the broods in the first year of oviposition — on the same condition as in the preceding case.
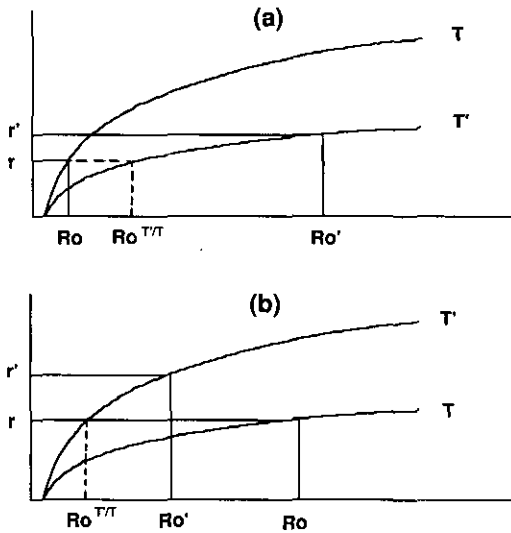
Fig. 3: Properties of the relation between r and Ro for different T values: (a) An increase in Ro (Ro' > Ro) leads to a higher r value in spite of a simultaneous increase in T (T' > T). (b): A decrease in T (T' < T) leads to a higher r value in spite of a simultaneous decrease in Ro (Ro' < Ro).

Adding that any decrease in r, due to a pleiotropic effect of some adaptation, cannot be ruled out at least temporarily, it is obvious that a wide range of possibilities exists, and it is a problem to know why some taxa have taken one path rather than another. But the solution clearly differs depending on whether the age or the stadium at the first oviposition has a genetic basis.

This is akin to the question of elongation and contraction, as pointed out by BLOWER (1969 b) as early as the 1st international Congress of Myriapodology. Elongation in the sense of VER-HOEFF (1928) is an evolution increasing Ro; contraction in the sense of BROLEMANN (1935) is an evolution decreasing T. The opinion of DOHLE (1988) that "both of these principles were at work, and that evolution could, after a period of elongation, lead once more to contraction", must be considered. From an ancestral type with a small number of rings, natural selection may have worked towards elongation. But, in addition to being limited, an increase in Ro may have made subsequent "contraction" easier in lineages having this genetic capacity; indeed, the higher Ro, the more favourable a decrease in T tends to be (Fig. 3). Conversely, a decrease in T is also limited under natural conditions with a periodical bad season: the life-cycle cannot be less than 1 year, unless one conceives an evolution towards polyvoltinism. Thus, elongation may be favoured in annual species, and this process might have occurred in some Craspedosomatida, from species coming to maturity in stadium VIII with 23 podous rings, to others with 25 podous rings.

3.2. K as a Measure of Fitness:

So far we have used the intrinsic rate of increase as a measure of fitness. Actually, the r-selection and K-selection concepts of MAC ARTHUR & WILSON (1967) assume that natural selection acts differently according to population density. At low density, resources being non-limiting, evolution favours productivity and r can measure fitness. On the contrary, in a crowded population, at or near the carrying capacity of the environment (K), resources being limiting, a high r value is no longer advantageous; the fittest genotypes are those which confer a maximum ability to exploit resources; evolution favours efficiency and K can be a measure of fitness.

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The life-history traits of species have been classified as r-selected or K-selected by a number of authors, referring to the theoretical correlates of both kinds of selection enumerated by PIANKA (1970). This classification has begun to be used in some studies on Diplopoda and, according to the correlates, early-maturing, short-lived, semelparous and small species might be rather r-selected, while late-maturing, long-lived, iteroparous and larger species might be rather K-selected.

Assuming that PIANKAs correlates are true, one wonders why there is a positive relationship between size and fecundity just in the so-called K-species (e. g. Cylindroiulinae). As far as K-selection is concerned, an increase in size should mainly lead to a better survival under competitive conditions, not to a greater reproductive ability. In the same way, one wonders why individuals are longer in populations of *T. niger* at a high altitude, where climatic conditions are less stable, and competition is likely to be less keen than in forests at a low altitude. *A priori*, it would seem that r is a better measure of fitness than K to deal with evolution in any Diplopod species.

However, it is difficult to make progress in the discussion without measuring population density, r-values and efficiency parameters (such as growth efficiency, P/I, the ratio of production to energy intake) in many cases. If we continued to base our arguments on the "correlates" of r- and K-selection in order to discuss the very existence of both these kinds of selection, we would be involved in a circular reasoning to the end of which we would never get.

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