ISSN 0240-8759

Vie et Milieu

Life and Environment

Vol. 46 nº 2 – Juin 1996

Périodique d'écologie - Publication trimestrielle

VIE ET MILIEU

Life and Environment

PÉRIODIQUE D'ÉCOLOGIE GÉNÉRALE
JOURNAL OF GENERAL ECOLOGY

LABORATOIRE ARAGO — UNIVERSITÉ P. et M. CURIE

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Publié avec le concours financier de l'Association Naturalia et Biologia

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ABONNEMENTS/SUBSCRIPTIONS 1996

	FRANCE	AUTRES PAYS
Un an (4 numéros) / *Annual subscription (4 issues)*.....	710 F	910 F

Adresser le paiement à l'ordre de / *Address payment to the order of :*

Vie et Milieu, Laboratoire Arago, 66650 BANYULS-SUR-MER. FRANCE

Les abonnements partent du premier numéro de l'année / *subscriptions begin with the first calendar year*

Numéros séparés de l'année, volumes antérieurs, suppléments et faunes des Pyrénées-Orientales, collections complètes, disponibles / *Back Issues and volumes, supplements and Faunas of Pyrénées-Orientales, complete collections, available :*

VIE ET MILIEU — Laboratoire Arago — F. 66650 BANYULS-SUR-MER

VIE MILIEU, 1996, 46 (2) : 103-114

ECOLOGICAL PHYLOGENETICS OF MATING SYSTEMS AND SEXUAL DIMORPHISM IN WATER STRIDERS (HETEROPTERA: GERRIDAE)

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MATING SYSTEMS
SEXUAL DIMORPHISM
COEVOLUTIONARY ARMS RACE
ECOLOGICAL PHYLOGENETICS
WATER STRIDERS
GERRIDAE

ABSTRACT. – Water striders of the heteropteran family Gerridae are conspicuously adapted for life on the water surface, especially with respect to locomotion, feeding, and reproductive behavior. Sexual dimorphism is usually pronounced in water striders. A basic, female-biased size dimorphism and a significant allometric relationship between sexual size dimorphism and overall size is well documented in temperate water strider species and is here extended to other species of the subfamily Gerrinae. Water striders are also dimorphic with respect to both primary and secondary sexual traits, especially shape and size of fore legs and structure of terminal abdominal segments and genitalia. In this paper the approach called ecological phylogenetics is used to study patterns of sexual dimorphism and mating systems in the monophyletic subfamily Gerrinae, focusing on the evolution of sexual dimorphism in relation to mating systems and the coevolution of male clasping and female anticlasper devices. There are no obvious, global phylogenetic effects or "constraints" on sexual dimorphism in the group, but phylogeny has played a certain role in shaping patterns of F/M size ratios, male clasping devices, and female anticlasper devices within clades. There is no support for the hypothesis that male and female genitalia and other structures have been involved in a coevolutionary "arms race". Finally, the phylogenetic effects on patterns of mating behavior are negligible as demonstrated by the large amount of interspecific variation in some genera, and by the fact that males of the same species may show alternative mating tactics depending on ecological circumstances.

SYSTÈMES D'ACCOUPLEMENT
DIMORPHISME SEXUEL
« COURSE À L'ARMEMENT »
COÉVOLUTIVE
PHYLOGÉNIE ÉCOLOGIQUE
GERRIS
GERRIDAE

RÉSUMÉ. – Les Hétéroptères de la famille des Gerridae sont manifestement bien adaptés à la vie à la surface de l'eau, particulièrement en ce qui concerne la locomotion, la nutrition et la reproduction. Le dimorphisme sexuel est généralement prononcé. Un dimorphisme de taille qui favorise la femelle et une relation allométrique significative entre le dimorphisme sexuel de taille et la taille totale concernant des espèces de Gerris des eaux tempérées sont bien connus et sont étendus ici aux autres espèces de la sous-famille des Gerrinae. Les Gerris montrent aussi un dimorphisme portant sur les caractères sexuels primaires et secondaires, particulièrement en ce qui concerne la forme et la taille des pattes antérieures, la structure des derniers segments abdominaux et les genitalia. Une approche par la phylogénie écologique, permettant d'étudier les modalités du dimorphisme sexuel et les systèmes d'accouplement dans la sous-famille des Gerrinae, qui est monophylétique, cerne l'évolution du dimorphisme sexuel lié aux systèmes d'accouplement et la coévolution des dispositifs d'appariement chez le mâle et de rejet chez la femelle. Il n'existe ni fardeau ni contraintes d'ordre phylogénétique sur le dimorphisme sexuel dans ce groupe, mais la phylogénie a joué un certain rôle sur la distribution des rapports de taille F/M, les dispositifs d'accrochage des mâles et de refus chez les femelles à l'intérieur des clades. Il n'y a pas lieu de supposer que les genitalia mâles et femelles ou les autres structures interviennent dans une «course à l'armement» coévolutive. Enfin, l'influence phylogénétique sur les modalités du comportement sexuel sont négligeables comme le montrent l'importance de la variation interspécifique chez certains genres ainsi que le fait que les mâles d'une même espèce puissent déployer des tactiques alternatives d'accouplement dépendant des conditions écologiques.

INTRODUCTION

Water striders of the heteropteran family Gerridae are conspicuously adapted for life on the water surface, especially with respect to locomotion, feeding, and reproductive behavior (Andersen, 1982a; Spence & Andersen, 1994). Their two-dimensional habitats make gerrids ideal objects for behavioral studies and recent interest in gerrid sexual behavior and strategies has focused on the three principal, Holarctic genera *Aquarius*, *Gerris*, and *Limnoporus*. Most species mate more frequently than necessary to ensure maximum fertility and males seem to contribute only sperm to offspring (Arnqvist, 1989b; 1995). The extremely long spermathecal tube typical of female gerrids (Andersen, 1982a; 1990; 1993b; Andersen & Spence, 1992), suggests that high rates of sperm displacement will be common, a prediction which has been confirmed experimentally (Arnqvist, 1988; Rubenstein, 1989; J. Spence, unpublished data).

Arnqvist (1995) suggested that matings in water striders can be divided into two distinct types. In Type I matings, males search actively for mates and when females are encountered, males initiate matings by simply lunging at and attempting to grasp females, without prior courtship. A male that is successful in achieving physical contact with a conspecific female will grasp the female's thorax with his forelegs, rapidly extend his genital segments, and attempt to insert his phallic organ into the genital opening of the female. Typically, females struggle vigorously before allowing intromission and are often successful in dislodging males (Arnqvist, 1989a; 1992a; Krupa *et al.*, 1990; Rowe, 1992; Rowe *et al.*, 1994; Weigensberg & Fairbairn, 1994). Males usually exhibit post-copulatory guarding, staying in close contact with the female after intromission is terminated (Andersen, 1982a; Arnqvist, 1995). Type II matings differ from type I matings in that males typically are territorial, defending suitable oviposition sites (Wilcox, 1972; Hayashi, 1985; Vepsäläinen & Nummelin, 1985b; Spence & Wilcox, 1986; Wilcox & Spence, 1986). There are much less apparent conflict and a reduced level of agression between sexes. Males, however, respond aggressively towards other males and engage in fights to defend their territory (Hayashi, 1985 and personal communication; Spence & Wilcox, 1986). Copulation is usually brief and type II matings typically involve post-copulatory non-contact guarding during which the female may oviposit. Using the commonly employed terminology of insect mating systems (Thornhill & Alcock, 1983), Arnqvist's (1995) type I matings can be characterized as "scramble competition polygyny" and type II matings as "resource defence polygyny" (Andersen, 1994; Spence & Andersen, 1994).

Sexual dimorphism is usually pronounced in water striders. Males are generally smaller than females except in the largest species. A basic, female-biased size dimorphism (female/male size ratio about 1.1) and a significant allometric relationship between sexual size dimorphism and overall size is well documented in temperate *Aquarius*, *Gerris*, and *Limnoporus* species (Fairbairn, 1990; Erlandsson, 1992; Andersen, 1994). Water striders are also dimorphic with respect to both primary and secondary sexual traits, especially shape and size of fore legs and terminal abdominal segments and genitalia (for examples see Matsuda, 1960 and Andersen, 1982a). Several authors have proposed that, given sexual conflicts over mating, male and female genitalia and other structures may be involved in a coevolutionary arms race (Parker, 1979; 1984; Arnqvist, 1995; Arnqvist & Rowe, 1995). This hypothesis predicts that males should evolve structures to cope with female resistance and that females should evolve structures to resist male harassment and to gain increased control over matings.

So far, studies of insect mating systems have chiefly been focused on single species or on comparisons among species without attention to their phylogenetic relationships. There have been few comparative studies of mating systems and associated structural features within monophyletic insect groups (groups that contain an ancestral species and all of its descendants). However, phylogenetic data can contribute significantly to studies of insect ecology and behavior by permitting inferences about the evolutionary history of traits (Brooks & McLennan, 1991; Harvey & Pagel, 1991; Eggleton & Vane-Wright, 1994; Spence & Andersen, 1994; Miller & Wenzel, 1995). This approach, ecological phylogenetics, is here used to study patterns of sexual dimorphism and mating systems in the monophyletic subfamily Gerrinae (Andersen 1975; 1982a; 1995), focusing on the evolution of sexual dimorphism in relation to mating systems and the coevolution of male clasping devices and female anticlasper devices.

METHODS

Size measurements and records of sexually dimorphic structures were obtained for 45 species (out of c. 160 described species) representing all 14 genera of the Gerrinae (Table 1). Male and female body size were measured (in mm) from the anterior margin of the head to the tip of the genital segments. Three types of data were used : (1) mean values for male and female body lengths

Table 1. – Total length of female (in mm), female/male (F/M) size ratio, male clasping devices (fore legs, genitalia), female anticlasper devices, and mating systems of water striders (Gerridae, Gerrinae). LW = long-winged adults, SW = short-winged or wingless adults. Definition of types of mating systems, see text.

Species	Wing morph	Female length	F/M ratio	Male clasping devices		Female anticlasper devices	Mating system	Source#
				Fore legs	Genitalia			
Limnoporus esakii	LW	10.0	1.25	no	no	yes	I	a
Limnoporus canaliculatus	SW	10.2	1.21	no	no	yes	I	b, c, l
Limnoporus notabilis	LW	18.1	1.04	no	no	yes	I, II	b, c, m
Limnoporus dissortis	LW	14.1	1.06	no	no	yes	I, II	b, c, m
Limnoporus rufoscutellatus	LW	15.5	1.09	no	yes	yes	I, II	d, n, o
Limnoporus genitalis	LW	13.8	1.10	yes	yes	yes	I	a, p
Aquarius najas	SW	16.5	1.28	yes	no	yes	I+	d, n, q
Aquarius cinereus	SW	12.7	1.32	yes	no	yes	I+	e, q
Aquarius remigis	SW	15.2	1.08	yes	yes	no	I+	f, r
Aquarius antigone	SW	13.4	1.17	yes	yes	yes	I	g, l
Aquarius paludum	SW	15.2	1.20	yes	yes	yes	I	d
Aquarius conformis	LW	16.5	1.09	yes	yes	yes	I+	f
Aquarius elongatus	LW	24.4	1.03	no	no	yes	I, II	h
Gerris incognitus	SW	9.5	1.12	yes	no	yes	I	f, s
Gerris nepalensis	SW	8.8	1.22	yes	no	yes	I	a, t
Gerris thoracicus	LW	13.5	1.13	yes	no	no	I	d
Gerris lacustris	SW	9.1	1.10	yes	no	no	I	d
Gerris latiabdominis	LW	10.9	1.16	yes	no	no	I	a, t
Gerris marginatus	LW	10.4	1.11	yes	no	no	I	i, u
Gerris comatus	SW	10.5	1.13	yes	no	no	I	f
Gerris odontogaster	SW	8.7	1.10	yes	yes	no	I	d
Gerris buenoi	SW	8.2	1.11	yes	no	no	I	f, v
Gerris argentatus	SW	7.3	1.19	yes	no	no	I	d
Gerris swakopensis	SW	7.1	1.15	yes	yes	yes	II	c, w
G. (Macrogerris) gracilicornis	LW	13.3	1.15	yes	no	no	I	a, t
G. (Gerriselloides) lateralis	SW	10.2	1.12	yes	no	no	I	d, x
Gigantometra gigas	LW	33.2	1.00	no	no	yes	?	c
Limnogonus fossarum	SW	8.7	1.23	yes	no	yes	I	c, g
Limnogonus buxtoni	SW	7.9	1.57	yes	no	no	?	j
Limnogonus windi	SW	6.5	1.18	yes	no	no	?	g
Limnogonus nitidus	SW	7.8	1.36	yes	no	yes	I+	c, j
L. (Limnogonoides) hypoleucus	SW	10.6	1.17	yes	no	yes	?	j
Tenagometrella grandiuscula	LW	13.3	0.85	no	no	yes	?	c
Tenagometra lanuginea	SW	7.5	1.14	yes	no	no	?	c
Tenagogonus albovittatus	SW	7.5	1.06	no	yes	no	I	c, x
Tenagogonus n.sp.	SW	8.8	1.18	no	no	no	?	g
Limnometra femorata	LW	16.6	0.80	no	no	yes	?	c
Limnometra cursitans	LW	13.4	0.86	no	no	yes	?	g
Limnometra anadyomene	LW	11.3	0.91	no	no	yes	?	c
Limnometra lipovskyi	SW	10.6	1.12	no	yes	yes	?	g
Tenagogerris euphrosyne	SW	9.1	1.30	yes	no	yes	I+	c, g
Gerrisella settembrinoi	LW	5.8	1.10	yes	yes	no	?	c
Neogerris parvulus	SW	5.0	1.22	yes	no	yes	I	c, j
Tachygerris surinamensis	LW	6.8	1.15	no	no	yes	?	k
Eurygerris cariniventris	SW	7.1	1.05	yes	no	yes	?	k
Eurygerris flavolineatus	SW	8.5	1.60	yes	no	no	?	c

Source : a, Miyamoto, 1958 ; b, Andersen & Spence, 1992 ; c, N.M. Andersen, unpublished ; d, Erlandsson, 1992 ; e, Andersen, 1990 ; f, Fairbairn, 1990 ; g, Andersen & Weir, in press ; h, Hayashi, 1985 ; i, Bennett & Cook, 1981 ; j, Andersen, 1975 ; k, Nieser, 1970 ; l, C. Klingenberg, unpublished ; m, Spence & Wilcox, 1986 ; n,Vepsäläinen, 1985 ; o, Vepsäläinen & Nummelin, 1985b ; p, J. Spence, unpublished ; q, Vepsäläinen & Nummelin, 1985a ; r, Rubenstein, 1984 ; s, Arnqvist & Rowe, 1995 ; t, Hayashi, 1992 ; u, Arnqvist, 1989a ; v, Rowe, 1992 ; w, Nummelin, 1988 ; x, Arnqvist, 1988.

obtained from the literature (sources listed in Table 1); (2) median values for ranges of body lengths obtained from the literature, and (3) mean values of actual measurements of specimens present in the Zoological Museum, University of Copenhagen. Size distributions usually approach normality in gerrids and the potential error introduced by using median rather than mean values for body lengths are therefore believed to be negligible. In order to simplify the analyses, measurements of adults representing different populations were pooled to yield estimates for each species. A potential source of error is therefore the relatively large between-population variation in F/M ratios recorded for some gerrids (Fairbairn, 1990; Erlandsson, 1992). Gerrids are usually polymorphic for wing development, with long-winged (LW), short-winged and/or wingless adults (collectively termed SW) in the same population (Andersen, 1982a; 1993a). For the purpose of interspecific comparisons, only measurements of SW individuals were considered (except

in some species of *Aquarius*, *Gerris*, *Limnoporus*, *Limnometra*, and *Tachygerris* which always are LW).

The phylogenies

Phylogenetic hypotheses are available for the genera of the subfamily Gerrinae (Andersen 1995), and for species or species groups of *Aquarius* (Andersen, 1990), *Gerris* (Andersen, 1993b), and *Limnoporus* (Andersen & Spence, 1992). Other phylogenetic relationships shown in the cladograms (Figs. 2-4) are based on a preliminary study involving all genera of Gerridae (N.M. Andersen, unpublished data). The subfamily Eotrechinae, the putative sister group of the Gerrinae (Andersen, 1982a; 1982b; Polhemus & Andersen, 1984), is used as outgroup in the phylogenetic analyses. The relationships depicted in a cladogram published by Calabrese (1980) are disregarded because they cannot be independently verified (Andersen, 1990; Andersen & Spence, 1992; Spence and Andersen, 1994).

The characters

The characters of interest in this paper are : (1) the female/male (F/M) size ratio; (2) male clasping fore legs; (3) male clasping genitalia; (4) female anticlasper devices; and (5) mating systems. The meaning of these characters and their states are explained below. Andersen (1994) used the "continuous variable" option of MacClade 3.0 (Maddison & Maddison, 1992) to map the distribution of residual F/M ratios on a phylogeny. In order to simplify the analyses of the present study, the observed range of F/M ratios was divided into four intervals which were scored as discrete states of one character : F/M ratio < = 1.04 (0); 1.05-1.14 (1); 1.15-1.24 (2); and > 1.25 (3). Characters (2)-(4) describing the state of male clasping and female anticlasper devices are simply scored as (0) absent or (1) present. Finally, the following states were recognized in character no. 5, mating systems (following Arnqvist, 1995) : type I (0); type I+ (with extended post-copulatory mate guarding) (1); and type II matings (2). These characters were optimized upon the phylogenetic hypotheses mentioned above. Sexually dimorphic traits, such as shape and size of fore legs and terminal abdominal segments, only constitute a small part of the total array of structural characters used to reconstruct these phylogenies. The basic assumption of independence between phylogenetic hypotheses and the traits of interest is therefore not seriously compromised.

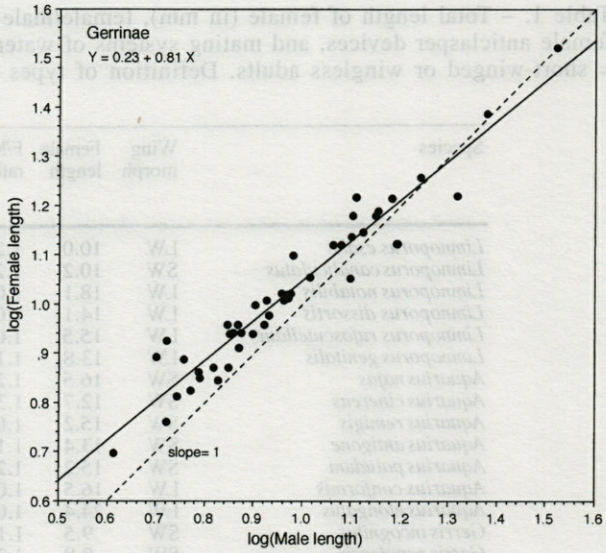

Fig. 1. – Regression plot of male length versus female length (both log-transformed) for selected species belonging to the subfamily Gerrinae (the species listed in Table 1). Regression lines for the actual relationship (slope = 0.81) and for isometric relationship (slope = 1) are also shown. Further discussion in text.

RESULTS

Optimization of sexually dimorphic characters

The variation in female body size and F/M ratio in selected gerrines is summarized in Table 1. Regression plots of male length versus female length (both log-transformed) are shown in Fig. 1 (based on the species listed in Table 1). The pattern of variation in F/M ratios optimized upon the phylogeny of the Gerrinae (Fig. 2A) indicates that a F/M ratio well below 1.25 is the ancestral state in the subfamily as it is in the outgroup Eotrechinae. Transitions to a F/M ratio above 1.25 have occurred in *Eurygerris flavolineatus* (Champion), *Tenagogerris euphrosyne* (Kirkaldy) (and two undescribed species of this Australian genus; Andersen & Weir, in press), *Limnogonus buxtoni* China and *L. nitidus* (Mayr) (Andersen, 1975), and in the *Aquarius najas* group (with four species; Andersen, 1990).

In species belonging to the subfamily Gerrinae, the fore femora are usually more robust in males than in females (Andersen, 1975; 1990; 1993b), curved and ventrally modified in *Eurygerris* and some *Tachygerris* species (Matsuda, 1960). The optimization of male fore leg structure on the gerrine phylogeny (Fig. 2B) suggests that fore legs modified for grasping is the ancestral state. Transitions to a state where the fore femora are slender in both sexes are observed in *Aquarius elongatus*, most *Limnoporus* species, in *Gigantometra gigas* (China) and in species of *Tenagogo-*

nus and *Limnometra*, which include some of the largest water striders (Hungerford & Matsuda, 1958; Matsuda, 1960; Hayashi, 1985; Andersen & Spence, 1992; Andersen & Weir, in press).

The gerrid male abdomen is composed of seven pregenital segments (only six visible on ventral side) and three genital segments which are withdrawn into the pregenital abdomen (Matsuda, 1960; Andersen, 1982a; 1993b). The genital segments are composed of the cylindrical segment 8 and the boat-shaped pygophore (segment 9) upon which lies the lid-shaped proctiger (segment 10). A pair of falciform parameres (genital claspers of Andersen, 1982a) are typically attached laterally to the edge of the pygophore. The phallic organ is hidden inside the pygophore when not inflated for copulation, and is composed of a sclerotized phallotheca and a membranous endosoma (or aedeagus), which again is divided into the conjunctivum and vesica. The latter has various sclerotized structures of great taxonomic importance (Andersen, 1975; 1990; 1993b; Andersen & Spence, 1992). Gerrine water striders lack large, clasping parameres, but many species have enlarged genital segments and various outgrowths or processes on the male terminal abdominal segments which may have a similar, clasping function. The optimization of male genital structure on the gerrine phylogeny (Fig. 3A) indicates that clasping genital structures have evolved in *Gerrisella settembrinoi* Poisson, *Tenagogonus albovittatus* (Stål), *Limnometra lipovskyi* Hungerford & Matsuda, *Limnoporus rufoscutellatus* (Latreille) and *L. genitalis* Miyamoto, in some *Aquarius* species, and in *Gerris odontogaster* (Zetterstedt) and *G. swakopensis* Stål (Hungerford & Matsuda, 1958; Matsuda, 1960; Andersen, 1990; 1993b; Andersen & Spence, 1992).

The gerrid female abdomen is composed of seven pregenital segments (only six visible on ventral side) (Matsuda, 1960; Andersen, 1982a; 1993b) and three genital segments which are inserted in the pregenital abdomen facing caudad and slightly ventrad. The large segment 8 is divided along the ventral midline into two, plate-shaped gonocoxae ("valvifers" of Matsuda, 1960); the eighth tergum carries the cone-shaped proctiger on its posterior margin. The ovipositor is normally concealed within segment 8, but is extended during oviposition. It is composed of two pairs of gonapophyses ("valvulae" of Matsuda, 1960) which form a tubular, egg-laying device. Female water striders have a very complicated internal reproductive system, the gynatrial complex, for the acceptance, storage, and distribution of sperm and fertilization of eggs. The gynatrial complex lies on top of the genital chamber and is typically composed of a gynatrial sac, an extremely long, tubular spermatheca, and a fecundation canal provided with a sperm pump (Andersen, 1975; 1982a; 1993b; see also Heming-Van Battum & Heming, 1986 for alternative interpretations of some structures).

The ancestral state of the female abdomen is probably one in which the ventral, posterior margin of segment 7 is simply concave, exposing the genital segments and genital opening. In many gerrines, however, the terminal segments of the female abdomen are variously modified in a way that may obstruct genital contact by the male, thus acting as anticlasper devices. The dorsolateral corners of segment 7 are commonly produced into spinose processes (connexival spines) which are very prominent in species of the genera *Limnometra*, *Tenagometrella*, *Gigantometra*, *Limnoporus*, and *Aquarius* species. The posterior margin of segment 7 is ventrally prolonged and/or modified to cover the genital opening in species of *Tenagogerris*, *Limnogonus*, *Eurygerris*, and *Tachygerris* (Matsuda, 1960; Andersen, 1975; 1990; Andersen & Spence, 1992; Andersen & Weir, in press). The optimization of female genital structures on the gerrine phylogeny (Fig. 3B) suggests that female anticlasper devices have been secondarily lost in *Neogerris, Gerrisella*, *Tenagogonus*, *Tenagometra*, some *Limnogonus* species, *Aquarius remigis* (Say), and in most *Gerris* species (Hungerford & Matsuda, 1958; Matsuda, 1960; Andersen, 1993b).

Optimization of mating systems

Observations of mating behavior, duration of copulation and post-copulatory guarding are only available for a little more than 30 species of water striders (Andersen, 1994; Arnqvist, 1995 and references therein), most of these belonging to the genera *Aquarius*, *Gerris*, and *Limnoporus*. Optimization of mating systems on the gerrine phylogeny (Fig. 4) indicates that the ancestral type of mating behavior for these genera as well as for the subfamily as a whole probably was "scramble competition polygyny" (type I matings of Arnqvist, 1995). Transitions to "resource defence polygyny" (type II matings of Arnqvist, 1995) have occurred independently in the *Limnoporus rufoscutellatus* group (Vepsäläinen & Nummelin, 1985b; Spence & Wilcox, 1986; Wilcox & Spence, 1986), *Aquarius elongatus* (Uhler) (Hayashi, 1985), and in *Gerris swakopensis* (Nummelin, 1988). Type I+ matings with extended post-copulatory guarding (guarding lasts for several hours or even days) occurs in the *Aquarius najas* group (Sattler, 1957; Vepsäläinen & Nummelin, 1985a; Murray & Giller, 1990) and in *A. conformis* (Uhler) (Fairbairn, 1990; Arnqvist, 1995). In *A. remigis*, pairs remain in copula for a long period of time (Wilcox, 1984; Clark, 1988; Rubenstein, 1989; Sih *et al.*, 1990; Fairbairn, 1990).

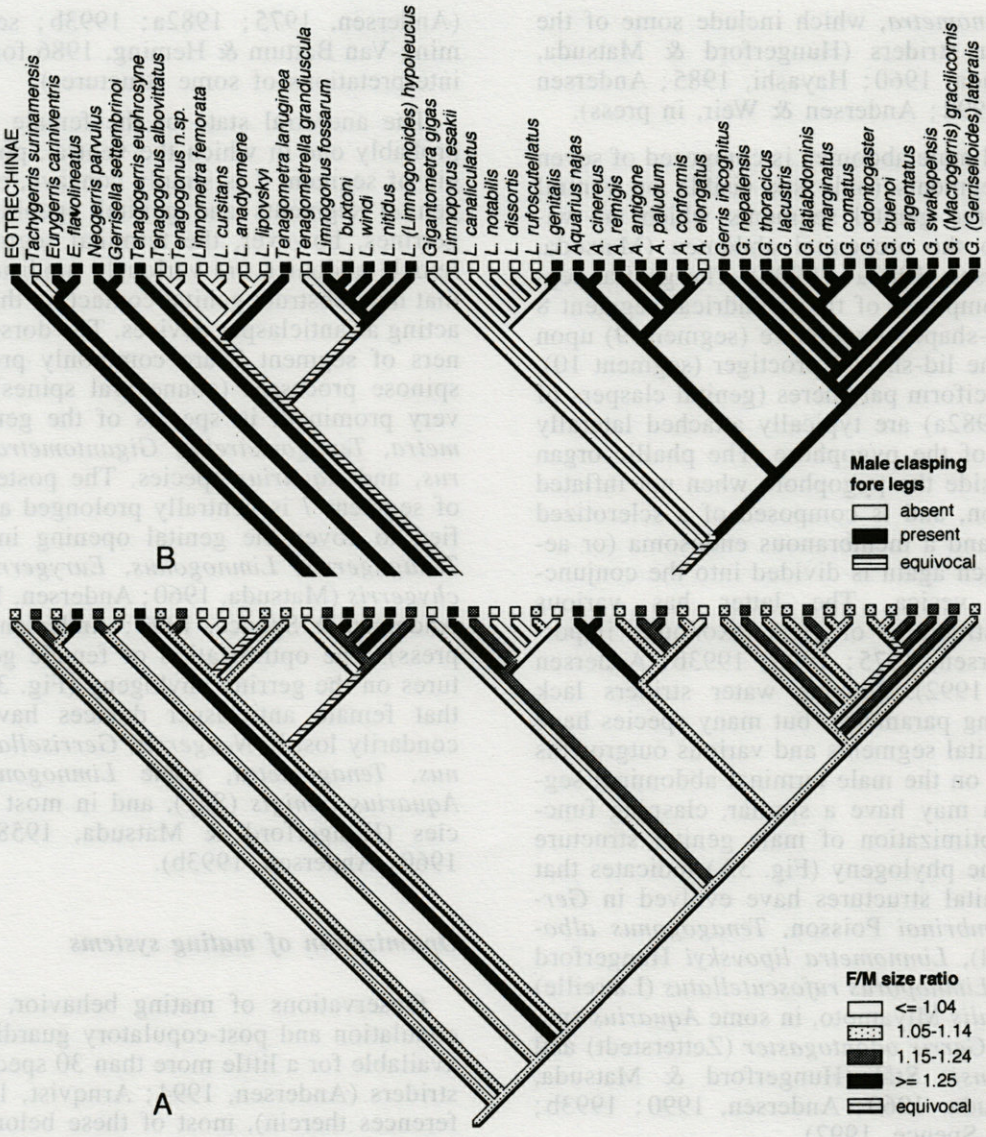

Fig. 2. – Optimization of (A) female/male (F/M) size ratios and (B) state of male fore legs (clasping versus non-clasping) on the reconstructed phylogeny of the Gerrinae. Further explanations in text.

The relationships between F/M ratio, male clasping devices, and mating systems

Gerrine water striders typically have male grasping fore legs (Fig. 2B), but the male fore femora of the larger species (*Limnometra* spp., *Tenagometrella grandiuscula, Gigantometra gigas*, the *Limnoporus rufoscutellatus* group, and *Aquarius elongatus)* are slender and seemingly not adapted for grasping the female's thorax. This usually coincides with F/M ratios about or below 1, which indicates that the male is as big as or even bigger than the female. Clasping devices of the male terminal abdominal segments (other than parameres) have secondarily evolved in *Gerrisella settembrinoi* and in some species of *Tenagogonus*, *Limnometra*, *Limnoporus*, *Aquarius*, and *Gerris*, all with a F/M ratio below 1.25 (Fig. 3A). Extended post-copulatory mate guarding is weakly associated with a large F/M ratio (*Tenagogerris euphrosyne*, *Limnogonus nitidus*, and the *Aquarius najas* species group) and with the absence of male clasping genitalia (but not grasping fore legs). Type II matings are weakly associated with non-grasping male fore legs and (in *Aquarius elongatus*) also with relatively unmodified male genitalia.

Coevolution of male clasping genitalia and female anticlasper devices

The presence of female anticlasper devices is not the ancestral state in the Gerridae but have

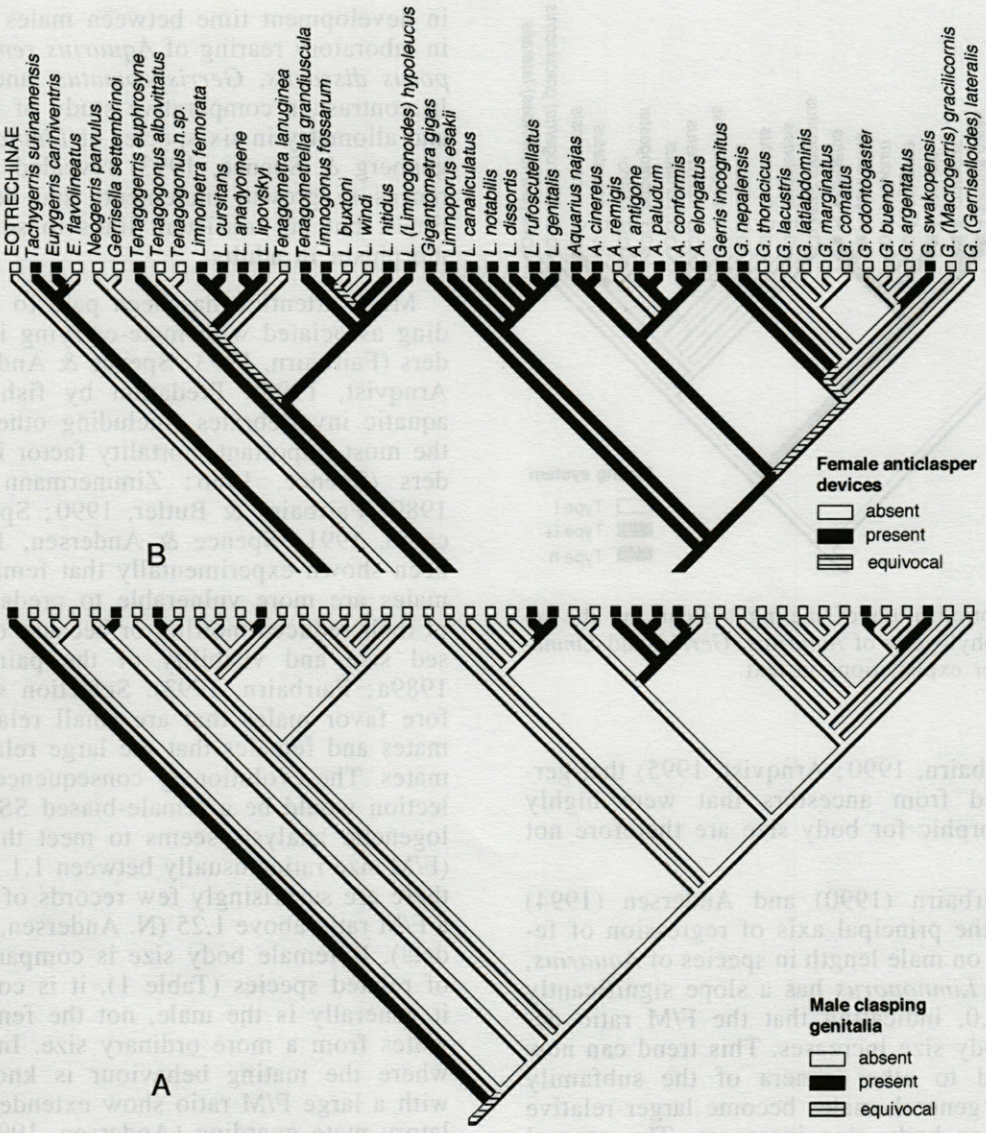

Fig. 3. – Optimization of (A) state of male genitalia (clasping devices absent/present) and (B) state of female terminal abdominal segments (anticlasper devices absent/present) on the reconstructed phylogeny of the Gerrinae. Further explanations in text.

evolved a number of times in the family, with or without the presence of male clasping genitalia (N. Andersen, unpublished data). Structures interpreted as anticlasper devices (connexival spines) have evolved in the absence of male clasping genitalia at the base of the Gerrinae (Figs. 3A and 3B), but have been secondarily lost in species of *Eurygerris, Neogerris* + *Gerrisella*, *Tenagogonus*, *Tenagometra*, *Limnogonus*, in *Aquarius remigis*, and in most species of *Gerris* s.lat. The presence of connexival spines in *Gerris incognitus* Drake & Harris, *G. nepalensis* (Distant), and *G. swakopensis* is interpreted as secondary. Thus, female anticlasper devices have been lost more often than they have evolved in the species studied and the association between male clasping genitalia and female anticlasper devices is not significant.

DISCUSSION

The largest species of Gerrinae (and of the whole family), *Gigantometra gigas*, is about 7 times as large as the smallest species belonging to the genus *Neogerris* (Table 1). Female/male size ratios varies between 0.8 for some species of *Limnometra* and 1.6 for *Limnogonus buxtoni* and *Eurygerris flavolineatus*. The phylogenetic analysis suggests that males of ancestral gerrines were primitively of about the same size or slightly smaller than conspecific females (F/M ratio between 1.0 and 1.15) and that a more pronounced sexual size dimorphism (F/M ratio above 1.25) has independently evolved several times in the subfamily. Previous suggestions (Andersen,

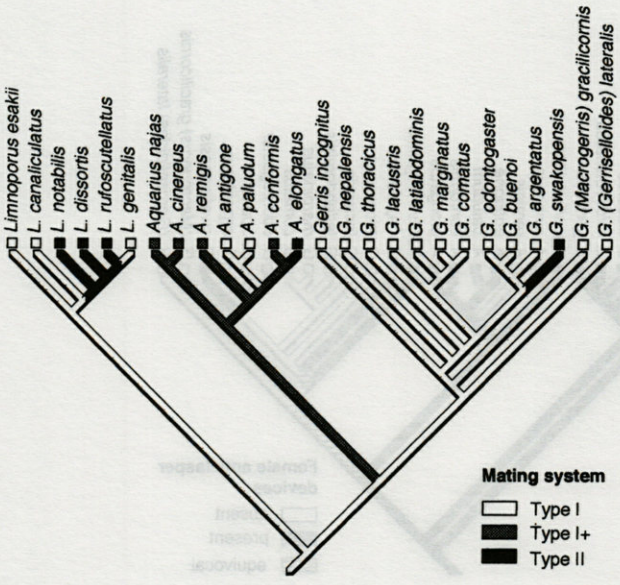

Fig. 4. – Optimization of mating systems on the reconstructed phylogeny of *Aquarius*, *Gerris*, and *Limnoporus*. Further explanations in text.

1982a; Fairbairn, 1990; Arnqvist, 1995) that gerrids evolved from ancestors that were highly sexual dimorphic for body size are therefore not supported.

Both Fairbairn (1990) and Andersen (1994) found that the principal axis of regression of female length on male length in species of *Aquarius*, *Gerris*, and *Limnoporus* has a slope significantly less than 1.0, indicating that the F/M ratio declines as body size increases. This trend can now be extended to other genera of the subfamily (Fig. 1). In general, males become larger relative to females as body size increases. The general conclusion of this study is that F/M ratios are highly variable within and between genera, and that there are no easily recognized, global phylogenetic effects or "constraints" on sexual size dimorphism in the Gerrinae. This confirms the conclusions by Fairbairn (1990) and Andersen (1994) based on smaller samples of species.

Several factors have been proposed to influence sexual size dimorphism (SSD) in water striders (Fairbairn, 1990; Andersen, 1994; Fairbairn & Preziosi, 1994; Spence & Andersen, 1994; Arnqvist, 1995; Blanckenhorn *et al.*, 1995). The general proposition that patterns of SSD are mainly nonadaptive outcomes of allometric growth is not necessarily valid for gerrids (Fairbairn, 1990; Andersen, 1994) and the correlated increase of leg lengths are of obvious importance since leg length is clearly an adaptive character in water striders (Spence, 1981; Andersen, 1982a; Fairbairn, 1992; Klingenberg & Zimmermann, 1992; Klingenberg & Spence, 1993; Fairbairn & Preziosi, 1994). Fairbairn (1990) found no significant differences in development time between males and females in laboratory rearing of *Aquarius remigis*, *Limnoporus dissortis*, *Gerris comatus*, and *G. buenoi*. In contrast, a comparative study of heterochrony and allometry in six species of *Limnoporus* (Klingenberg & Spence, 1993) revealed sexual differences in growth increments and developmental times, but no consistent links to sexual size dimorphism in adults.

Much attention has been paid to costs of loading associated with mate-carrying in water striders (Fairbairn, 1993; Spence & Andersen, 1994; Arnqvist, 1995). Predation by fish, frogs, and aquatic invertebrates (including other gerrids) is the most important mortality factor in water striders (Spence, 1986; Zimmermann & Spence, 1989; Fairbairn & Butler, 1990; Spence & Cárcamo, 1991; Spence & Andersen, 1994). It has been shown experimentally that females carrying males are more vulnerable to predation because of their reduced motility or because of the increased size and visibility of the pairs (Arnqvist, 1989a; Fairbairn, 1993). Selection should therefore favor males that are small relative to their mates and females that are large relative to their mates. The evolutionary consequence of such selection would be a female-biased SSD. The phylogenetic analysis seems to meet this prediction (F/M size ratios usually between 1.1 and 1.2), but there are surprisingly few records of gerrids with a F/M ratio above 1.25 (N. Andersen, unpublished data). If female body size is compared with that of related species (Table 1), it is concluded that it generally is the male, not the female that deviates from a more ordinary size. In those cases where the mating behaviour is known, species with a large F/M ratio show extended post-copulatory mate guarding (Andersen, 1994; Arnqvist, 1995), a situation where the loading costs are assumed to be highest. An alternative explanation of the advantage of small male size has recently been offered by Blanckenhorn *et al.* (1995) based on the hypothesis that selection favors small males because they use less energy in maintaining activity and therefore may devote more time to search for mates.

The present phylogenetic analysis suggests that males of ancestral water striders had powerful fore legs adapted to grasp the female's thorax during mating, and had clasping genitalic structures suited to grasp or pinch the female posteriorly. It is also suggested that females of these ancestral gerrids had relatively unspecialized terminal abdominal segments. The ancestral and most common mating system in gerrine water striders has been categorized as "scramble competition polygyny" (Thornhill & Alcock, 1983; Andersen, 1994; Spence & Andersen, 1994; "type I matings" of Arnqvist, 1995) and is characterized by apparent conflicts and dramatic struggles,

where the male tries to gain control over the female which respond with vigorous resistance. It is argued in several recent papers (Rowe *et al*, 1994; Arnqvist, 1995 and references therein) that the predominant mating system in water striders is a direct consequence of sexual conflicts over mating decisions. Matings involve high costs to females (risk of predation and energetic expenditure) but very few, if any, benefits. Relatively few matings are enough for a female to get all of her eggs fertilized. Females are therefore under selection not to mate (Parker, 1979). In contrast, the reproductive success of males is associated with the number of females they mate. Since sperm displacement rates seem to be high in gerrids (Arnqvist, 1988; Rubenstein, 1989, J. Spence, unpublished data), the last male to mate will fertilize most of the female's eggs. Thus, there is a strong selective advantage in males to reduce sperm competition by guarding a female for a certain period of time. Typically, the male rides passively on the female's back during guarding, but in *Limnogonus nitidus* the male is positioned far back on the female and is towed around (Andersen, 1982a and unpublished data). In *Aquarius elongatus* and probably in other species where the male is the larger sex, the male carries the passive female beneath (Hayashi, 1985 and personal communication). Males normally retract their phallic organ during guarding, but *Aquarius remigis* males prolong copulation beyond the time necessary for sperm transfer, thus acting as living mating plugs (Wilcox, 1984; Clark, 1988; Rubenstein, 1989; Sih *et al.*, 1990; Fairbairn, 1990). The prolonged phallic vesica of this species may be an adaptation to that function (Matsuda, 1960).

Direct empirical evidence on sexual selection for body size in water striders is scarce and partly contradictory (Arnqvist, 1995). Females should allow small males to mate longer due to reduced costs of loading (Fairbairn, 1993), but most studies actually show sexual selection for large males (Hayashi, 1985; Fairbairn, 1988; Sih & Krupa, 1992; Krupa & Sih, 1993; Fairbairn & Preziosi, 1994). Large males should be better able to subdue reluctant females and in species where the male is the larger sex, males are known to carry the females during copulation (Andersen, 1982 and unpublished data). A phenomenon which needs further exploration is the extraordinary large variance in male size reported in some water strider species, e.g., *Limnometra anadyomene* (N. Andersen, unpublished data), *L. lipovskyi* (Andersen & Weir, in press), and *Tenagometra lanuginea* (Andersen, 1982a).

It is assumed that males with the more powerful fore legs are better able to grasp the female's thorax during copulation and sexual selection for more incrassate femora has been experimentally demonstrated in *Aquarius remigis* males (Rubenstein, 1984). The terminal abdominal segments and genitalia are modified in many water striders, provided with outgrowths and processes of various shape and large, clasping parameres (Matsuda, 1960; Andersen, 1982). It is assumed that such modifications function as claspers during copulation. In *Gerris odontogaster*, males are provided with paired, tooth-like processes on the venter of the seventh abdominal segment (Arnqvist, 1989b; Andersen, 1993b). Through a series of studies, Arnqvist (1989a; 1989b; 1992a; 1992b; 1992c; 1994) has convincingly demonstrated that these structures are critical for males in enduring the pre-copulatory struggle by the female, and hence achieve more matings both in the laboratory and the field. Thus, in *G. odontogaster* there is sexual selection by female choice for long ventral teeth with a clasping function. More casual observations suggest that many, if not all, modifications of the male genitalia in water striders have a similar function (Andersen, 1982a).

Several authors have proposed that, given sexual conflicts over mating decisions, females should evolve counter-adaptations to cope with sexual harassment and to gain increased control over matings (Parker, 1979; 1984; Eberhard, 1985; Arnqvist, 1995). The connexival spines of *Gerris incognitus* females have been found to function in this way. By manipulating the length of these spines Arnqvist & Rowe (1995) showed that the spines increase female ability to dislodge males during the pre-copulatory struggle, and thus gain increased control over mating decisions. As shown in the present study, a number of structures of the terminal abdominal segments of females are potential candidates for a similar function. If such traits represent "counter-adaptations" to enable females to control matings by making it more difficult for males to establish genital contact, one should expect that such anticlasper devices had evolved at the same time or immediately after the evolution of male genital clasping devices. Comparisons between the optimization of female and male traits on the reconstructed phylogeny of the Gerrinae (Figs. 3A and 3B) suggest that female anticlasper devices (especially connexival spines) have evolved in the absence of male clasping genitalia in this subfamily. In this sense, females seemingly have taken the lead in the "arms race" between sexes. However, by making it costly for females to resist matings (e.g., when harassment rates are high), males may be said to have won the "battle of the sexes" (Arnqvist, 1995). Thus, the hypothesis of an evolutionary "arms race" between sexes cannot be unambiguously tested, at least not for the Gerrinae.

Type II matings (Arnqvist, 1995) or "resource defence polygyny" (Thornhill & Alcock, 1983; Andersen, 1994; Spence & Andersen, 1994) see-

mingly evolved from type I matings at least four times during the evolutionary history of the Gerridae : (1) in the genus *Rhagadotarsus* (Wilcox, 1972; Nummelin, 1988; N. Andersen, unpublished data); (2) in *Aquarius elongatus* (Hayashi, 1985); (3) in species of *Limnoporus* (Spence & Wilcox, 1986; Wilcox & Spence, 1986); and in *Gerris swakopensis* (Nummelin, 1988). It should be emphasized, however, that sexual behavior used to categorize mating systems are not at all rigid and that both males and females may use alternative behaviors. For instance, *Aquarius elongatus* shows both type I and type II as well as intermediate mating behavior varying through the season (Hayashi, 1985, and personal communication). Spence & Wilcox (1986) also showed that males of both *Limnoporus dissortis* and *L. notabilis* employ the full range in mating behavior. Finally, observations of *Gerris swakopensis* in the laboratory suggest that males are not necessarily territorial either (J.R. Spence, unpublished).

Arnqvist (1995) suggested that sexual conflicts has played a crucial role in the evolution of type II mating behavior from type I matings. As in other insects, female water striders are particularly sensitive to male harassment during oviposition. In cases where type II matings are involved, males provide females with oviposition sites and protect them from harassment by other males. Female *Limnoporus* were found to lay more eggs if protected by a guarding male (Spence & Wilcox, 1986). If females, in order to achieve such protection, evolve traits (behavioral and/or structural) that increase their control of mating initiation, it may be more profitable for males to be more sedentary and to "court" rather than harass females. In type II matings, males are typically territorial, defending suitable oviposition sites, seeking to attract females by surface ripple signals (Wilcox, 1972; Hayashi, 1985; Wilcox & Spence, 1986; Nummelin, 1988). Males of *Aquarius elongatus* respond aggressively towards other males and engage in fights to defend their territory. The middle legs of the male (which are relatively longer than in the female) are used as weapons during such fights, but I suggest that they also may have an "ornamental" function during the courtship (Hayashi, 1985 and personal communication). Sexual differences in the middle and/or hind legs of *Gigantometra gigas* and some *Limnometra* species (Hungerford & Matsuda, 1958; Andersen, 1982a; Andersen & Weir, in press) may suggest a similar function.

In conclusion, there is a considerable interspecific variation in sexual dimorphism and mating behavior in water striders belonging to the subfamily Gerrinae. There are no obvious, global phylogenetic effects or "constraints" on sexual dimorphism in the group, but phylogeny has played a certain role in shaping patterns of F/M size ratios, male clasping devices, and female anticlasper devices within clades. There is no support for the hypothesis that male and female genitalia and other structures have been involved in a coevolutionary "arms race". Finally, the phylogenetic effects on patterns of mating behavior are negligible as demonstrated by the large amount of interspecific variation in some genera (e.g., *Limnoporus*, *Aquarius*, and *Gerris*), and by the fact that males of the same species may show alternative mating tactics depending on ecological circumstances (Spence & Andersen, 1994). Many aspects of the biology of water striders make them ideal for both comparative and experimental behavioral studies and a growing literature has proven water strider to be well suited to address many general issues about the evolution of mating systems. I hope that this paper will stimulate additional, taxonomically broadly based studies of sexual dimorphism and mating systems in this group of insects.

ACKNOWLEDGMENTS – I thank K. Hayashi, C. P. Klingenberg, and J. R. Spence for letting me use their unpublished data. I also thank G. Arnqvist and J. R. Spence for reviewing the manuscript and offering constructive remarks. The work was supported by operating grants awarded by the Danish Natural Science Research Council (Grant Nos. 11-0090 and 9502155).

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LE CLADISME, TRENTE ANS APRÈS *PHYLOGENETIC SYSTEMATICS*; QUELQUES REMARQUES À PROPOS DE DÉBATS RÉCENTS

Cladistics, thirty years after Phylogenetic Systematics : *some recent conflicts*

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J'ai comme un remords de vieille analyse,
Dont pour la comprendre il faut que je lise
Les termes précis dans un vieux bouquin :
N'écrivez donc pas, c'est bien plus malin

Edouard Cumenge,
Géologie et généalogie

CLADISME
PHYLOGÉNIE
PARCIMONIE
PHÉNÉTIQUE
HENNIG

RÉSUMÉ. – Des points de vue très contrastés existent toujours parmi les systématiciens sur la qualité de l'approche cladistique, trente ans après la publication de *Phylogenetic Systematics* de Willi Hennig. On discute dans cet article de quelques critiques récentes pour faire la part de ce qui témoigne d'une méconnaissance de la nature profonde de l'analyse cladistique et de ce qui s'applique effectivement aux limitations des approches de parcimonie.

CLADISTICS
PHYLOGENY
PARSIMONY
PHENETICS
HENNIG

ABSTRACT. – Very different viewpoints on the virtues of cladistics can be found among taxonomists, thirty years after the issue of Willi Hennig's *Phylogenetic Systematics*. In this paper some recent critiques are discussed. These critiques are separated in two kinds, those which are a consequence of a misunderstanding of the basic nature of cladistic analysis, and those which apply to the limits of parsimony procedures.

Il y a vingt ans disparaissait Willi Hennig, inventeur de la systématique phylogénétique. Pour certains, dont je suis, la lecture de *Phylogenetic Systematics* (Hennig, 1966) fut une expérience comparable à celle de *l'Origine des espèces* de Darwin. Pour d'autres, la systématique phylogénétique, ou cladisme si l'on préfère, n'est qu'une approche parmi d'autres, pas plus attractive ni plus nécessaire que les autres.

Faut-il rappeler le but poursuivi par Hennig ? Brièvement, selon ce dernier, la classification des êtres organisés ne devait être que l'expression formalisée de la phylogénie. Ce faisant, Hennig proposa un corpus méthodologique de reconstruction phylogénétique. L'œuvre de Hennig est fondée sur un constat en apparence banal : la simple ressemblance globale ne donne pas la filiation, celle-ci n'est indiquée que par l'homologie à son niveau de synapomorphie à l'issue d'une analyse des caractères pris individuellement. Les mots-clefs du « hennigisme » sont : apomorphie, plésiomorphie, monophylie, paraphylie, groupes frères. La systématique phylogénétique permet 1) de reconnaître les taxons ayant une dimension phylogénétique – les clades ou groupes monophylétique –, 2) de les définir d'un point de vue diagnostique (grâce au concept de synapomorphie), et 3) de les nommer au moyen de règles nomenclaturales.

Des points de vue très contrastés existent quant à l'appréciation de l'œuvre de Hennig et de la pratique actuelle de la cladistique. Il y a peu, on pouvait lire dans les colonnes d'une revue de référence, *Systematic Biology*, qu'en matière de méthodes de reconstruction phylogénétique, la cladistique était la plus utilisée, notamment par le biais de son application informatisée, dite méthode de parcimonie (Sanderson *et al.*, 1993). Par ailleurs, Allard (1993) remarquait, à l'occasion d'une

revue d'un important volume collectif consacré aux phylogénies moléculaires (Miyamoto & Cracraft eds., 1991), que les articles reposant sur une analyse de caractères étaient plus nombreux que ceux reposant sur une analyse de distance, ce qui était interprété comme un signe de la prééminence des analyses de parcimonie.

Dans le même temps, deux constats sans appel qualifiaient l'analyse cladistique de méthode de peu d'intérêt, voire nulle et non avenue : « The real weakness of the parsimony approach is that it does not contain a testable scientific hypothesis. Its use does not follow the standard scientific procedure of setting up a model that can be tested empirically, and rejected or modified if necessary » (Cavalli-Sforza *et al.*, 1994 : 34) ; et aussi : « Hennigian cladistics, however, is a side issue that has not proven its value » (Sneath 1995 : 281). Est-ce à dire que les praticiens font erreur depuis tant d'années ? Que le succès des analyses hennigiennes puis des logiciels dits de parcimonie tels que PAUP (Swofford 1990) ou Hennig86 (Farris, 1988) n'est dû qu'à la cécité des utilisateurs ? En réalité, il faut bien saisir d'où viennent ces commentaires négatifs : de la sphère de la taxinomie numérique (ou phénétique si l'on préfère cette dénomination), une autre pratique de la systématique, qui, à la manière du cladisme, a vocation à l'universel. En effet, les deux approches se sont présentées, chacune en son temps, comme le système de référence général. De fait, on peut lire aujourd'hui les mêmes appréciations peu flatteuses à l'égard de la taxinomie numérique. Par exemple Nelson (1994 : 11) considère aujourd'hui que « tout l'épisode phénétique de la systématique confirme le point de vue ancien de Ross (1964 : 108) selon lequel la phénétique est une « excursion dans la futilité ». Comme on le voit, il reste quelque chose de la vivacité des débats du passé. Un mot sur le poids des mots : j'écris « phénétique » comme autre qualificatif de la « taxinomie numérique » mais ce terme, fort usuel dans la littérature francophone (mais pas seulement, voir Forey *et al.*, 1992) est critiqué. L'expression « méthode statistique » est parfois revendiquée aujourd'hui pour qualifier la phénétique (Sidow, 1994 ; Hugues, 1994), la noblesse scientifique de l'adjectif « statistique » paraissant manifestement un argument de poids pour convaincre de la valeur de la méthode. La statistique est-elle pour autant l'apanage de cette systématique-là, plutôt que des autres ? Rien n'est moins sûr comme il a été montré dans un récent forum (Stewart, 1994).

En dernier lieu, un débat figurant dans la rubrique « technical comments » de la revue *Science* – le dernier en date, à l'heure où j'écris – résume assez bien la nature plurielle des arguments. A la suite de comparaisons des performances respectives des différentes méthodes concurrentes dont les conclusions étaient plutôt favorables aux procédures de parcimonie (Hillis *et al.*, 1994), étaient publiées deux réactions argumentées en forme de dénégations contradictoires (Edwards, 1995 ; Nei *et al.*, 1995). Ce débat là est exemplaire et j'y reviendrai.

Que des auteurs aussi considérables que Cavalli-Sforza et Sneath rejettent sans ménagement la cladistique aux oubliettes de la systématique ou bien que d'autres auteurs, tout aussi considérables, tels Edwards et Nei, se sentent tenus de « monter au créneau » afin de minorer des conclusions favorables à la meilleure efficacité des procédures de parcimonie ne peut qu'influencer, d'une manière ou d'une autre, les systématiciens. Il me paraît donc nécessaire de réfléchir un temps sur ces positions. A mon sens, au-delà de la discussion sur les limites du cladisme (car les limites des autres méthodes sont tout aussi péremptoires), ces jugements sur l'analyse cladistique témoignent à la fois d'une stratégie de persuasion et d'une méconnaissance de la nature profonde du cladisme. J'essayerai de montrer dans cet article que loin d'assister à l'extinction du cladisme, nous n'en voyons au contraire que les prémisses. L'amélioration des méthodes de reconstruction phylogénétique que les systématiciens appellent de leurs vœux sera d'abord l'amélioration de la procédure cladistique et non son rejet.

Stratégie de persuasion

La rhétorique n'est jamais absente des démonstrations scientifiques, notamment s'il s'agit de convaincre de la supériorité d'une méthode sur une autre. On peut s'attendre à ce que des auteurs qui ont jeté, dans les années soixante, les bases de la phénétique, tels Cavalli-Sforza et Sneath, ne reviennent pas aisément sur leurs positions, d'autant qu'effectivement un nombre considérable de travaux se réclamant de la phénétique ont vu le jour depuis, et continuent à être publiés. Plus encore, l'utilisation des données moléculaires a donné un second souffle – voire un tout autre sens – à la taxinomie numérique. Si le succès populaire est un critère d'efficacité il n'y a, à n'en pas douter, aucune raison de pratiquer une quelconque autocritique, bien au contraire. Selon Sneath (1995 : 281) la taxinomie numérique est « the greatest advance in systematics since Darwin or perhaps since Linnaeus ». Quant à Cavalli-Sforza *et al.* (1994), après que l'analyse de parcimonie ait encouru le reproche de ne pas être une entreprise scientifique selon les termes cités plus haut, le choix de la méthode utilisée dans leur travail, l'UPGMA de Rohlf et Sokal, se résumait à une seule raison : cette méthode est la plus populaire.

D'autres, pourtant, ont suivi un chemin différent. Issus de la sphère de la taxinomie numérique,

ils se sont peu à peu orientés vers des approches ressortissant à l'analyse cladistique. Deux auteurs sont représentatifs, à bien des égards, de cet itinéraire et l'ont expliqué eux-mêmes dans deux articles remarqués : Farris (1977) et Fitch (1984). Le premier a conçu au début des années soixante-dix des stratégies de construction d'arbres au moyen de distances, c'est-à-dire relevant de la taxinomie numérique (Farris, 1972) tout en publiant, par ailleurs, l'algorithme de parcimonie dit de Wagner (Kluge & Farris, 1969; Farris, 1970). Le second préconisa une méthode de distance (Fitch & Margoliash, 1967) qui eut un impact si considérable sur les pratiques phylogénétiques qu'elle fut communément nommée méthode de Fitch-Margoliash et pendant longtemps fut la plus utilisée parmi les méthodes phénétiques. Dans le même temps, néanmoins, Fitch mettait également au point un algorithme de parcimonie (Fitch 1970).

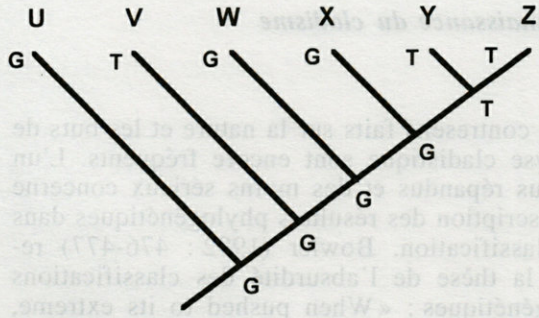
On rencontre ainsi des itinéraires opposés chez de brillants esprits. C'est donc au-delà des professions de foi qu'il faut essayer de comprendre les raisons de ces points de vue aussi nets que contradictoires. Les théoriciens n'échappent pas à leur pratique : revendiquer, à vingt ans d'écart (Sneath & Sokal, 1973; Cavalli-Sforza *et al.*, 1994), l'UPGMA comme *la* méthode de référence en matière de construction phylogénétique n'est compréhensible que si l'on tient compte des objets étudiés : les Bactéries pour Sneath, les populations humaines pour Cavalli-Sforza. Les Bactéries représentent un défi pour les systématiciens évolutionnistes, depuis la notion d'espèce jusqu'à celle d'arbre phylogénétique. De la sorte, l'obtention de clusters phénétiques est déjà un résultat appréciable, sans qu'il soit nécessaire de travestir ces clusters du nom de clade. L'histoire des populations au travers de l'analyse des fréquences géniques, qui est l'objet de l'étude de Cavalli-Sforza et de ses collaborateurs, est aux limites de l'applicabilité de l'analyse cladistique, qu'il s'agisse de la question des fréquences, ou bien de la pertinence de la notion de phylogénie appliquée à des populations. Le vivant est ce qu'il est, les méthodes sont ce qu'elles sont : à la diversité du vivant répond la diversité des méthodes. Certaines données peuvent être analysées de façon cladistique, d'autres non. Ce constat serait très banal et guère propice à entretenir des débats si la nature de ces données ne posait pas en réalité le problème de la signification profonde de la construction phylogénétique. Quelle est la spécificité des relations phylogénétiques vis-à-vis de tout autre type de relations ? Qu'est-ce qui fait qu'un arbre puisse être qualifié de phylogénétique ? Qu'est-ce qui permet d'identifier un clade ? C'est pourquoi bien des critiques faites aujourd'hui à l'analyse cladistique relèvent plus de l'incompréhension que de la proclamation triomphante.

Méconnaissance du cladisme

Des contresens faits sur la nature et les buts de l'analyse cladistique sont encore fréquents. L'un des plus répandus et des moins sérieux concerne la transcription des résultats phylogénétiques dans une classification. Bowler (1992 : 476-477) reprend la thèse de l'absurdité des classifications phylogénétiques : « When pushed to its extreme, cladism implies that – since the birds and other Reptiles share a common ancestor – then birds are reptiles and should not be designated as a separate class. » Vis-à-vis de la phylogénie, c'est bien le statut des Reptiles qui pose problème (et implicitement celui des Crocodiles) et non le rang accordé aux Oiseaux dans la classification. Les Reptiles ont un sens évolutif, ils forment un grade, mais ne sont tout simplement pas une entité à contenu phylogénétique – un clade – comme on le sait depuis le fameux dialogue entre Mayr (1974) et Hennig (1974) et comme Goodrich, en 1916, l'avait déjà montré dans les mêmes termes.

S'il fallait résumer par un seul mot l'apport de Hennig à la systématique, je choisirais, avec Nelson (1994), celui de « paraphylie ». Dans une perspective évolutionniste, ce concept permet, mieux que tout autre, d'opposer grades et clades et de faire la part de ce qui a une dimension phylogénétique, les clades, de ce qui n'en a pas. Il est piquant de relire sous la plume de Sneath (1995 : 287) un vieil argument selon lequel « the problem of paraphyletic groups is not easily disposed of by Hennigian cladistics », alors que la compréhension même de la paraphylie ne peut se concevoir que dans le cadre de la problématique cladistique. On le sait : est un groupe paraphylétique celui dont les membres ne partagent que des caractères plésiomorphes. Une telle définition implique qu'un groupe paraphylétique ne peut être reconnu comme tel qu'à l'intérieur d'un système fondé sur la partition des caractères entre apomorphes et plésiomorphes. C'est pourquoi les analyses de similitude globale (ou de distance, comme on voudra), qui ne font aucune distinction entre les classes de similitude, sont incapables de faire la distinction entre regroupements dûs à l'apomorphie ou à la plésiomorphie. La méthode UPGMA est notoirement connue pour regrouper les taxons sur la base de la plésiomorphie, c'est-à-dire construire des clusters qui peuvent correspondre, en analyse cladistique, à des groupes paraphylétiques. En l'occurrence, le seul problème (il est de taille) des méthodes de distance est qu'elles ne permettent pas de savoir quand un cluster phénétique correspond, dans une perspective évolutionniste, à un grade (éventuellement un groupe paraphylétique) ou bien à un clade.

Il convient de rappeler que les méthodes phénétiques ont d'abord été conçues pour construire



	66
U	G
V	T
W	G
X	G
Y	T
Z	T

Fig. 1. – Synapomorphie et homoplasie : distribution des états d'un caractère (site 66) sur un cladogramme (U-Z = taxons terminaux ; G = guanine, T = thymine).

Synapomorphy and homoplasy : character state distribution of site 66 on a cladogram (U-Z = terminal taxa ; G = guanine, T = thymine).

des classifications étrangères à la sphère des idées évolutionnistes (Sneath & Sokal, 1973). L'un des principaux arguments était que la phylogénie était inconnaissable et que la recherche des homologies ressortissait à un raisonnement circulaire : il fallait connaître l'histoire de l'évolution afin d'identifier les homologies et, en même temps, ces dernières servaient à identifier l'histoire de l'évolution. De la sorte, seule la ressemblance pouvait être mesurée en toute certitude. On le sait, la circularité invoquée ne repose que sur la présentation partielle du concept d'homologie. D'autre part, dans une perspective évolutionniste, le traitement de la ressemblance globale ne suffit pas à construire un arbre phylogénétique. La partition apomorphie / plésiomorphie est compliquée par la partition homologie / homoplasie. C'est pourquoi, en taxinomie numérique même, des méthodes de distances furent avancées qui cherchaient à réduire les risques de regrouper les taxons sur la base de la plésiomorphie, à l'instar de la méthode de Fitch & Margoliash (1967). Restait la gestion de l'homoplasie, qui ne pose un réel problème que dans le cadre de la reconstruction phylogénétique puisque le concept est lié à la théorie de l'évolution. Qu'on le veuille ou non, seuls les algorithmes dits de parcimonie font cette partition et localisent homologies et homoplasies sur l'arbre. L'itinéraire d'un évolutionniste tel que Ernst Mayr vis-à-vis de la phénétique et de la cladistique est révélateur à cet égard (Mayr, 1974, 1986 ; Mayr & Ashlock, 1991). Qu'une telle entreprise soit légitime ou bien efficiente en termes informatiques est un autre problème. La légitimité réside dans les nécessités de la systématique : l'identification des homologies ; l'efficience est un problème technique sur lequel je reviendrai plus loin.

L'analyse cladistique traite les caractères discontinus. On ne s'étonnera pas que les défenseurs des méthodes de distance se retrouvent chez les utilisateurs de caractères continus, comme les fréquences géniques. Il existe d'ailleurs des moyens de coder des caractères continus sous forme de caractères discrets, un procédé fort discuté (voir notamment Thiele, 1993). On peut aussi concevoir les choses autrement. En analyse cladistique une transformation de caractère est assimilée à un événement évolutif. Peut-on en revanche assimiler *a priori* les variations des fréquences géniques à des événements historiques ? Faute d'un consensus autour de cette question, il est patent que ce type de données est le plus souvent traité par des méthodes de distances.

A mes yeux, et à ceux des cladistes en général (Nelson, 1994), ce qui singularise fondamentalement la méthode cladistique (ou de parcimonie) est sa nature phylogénétique parce que fondée sur le principe de l'homologie au sens évolutionniste du terme : l'homologie due à l'ascendance commune (Darwin, 1872 : 517). Il est inutile d'avancer 1) que l'analyse de parcimonie peut donner des résultats erronés, 2) que l'on n'est jamais sûr qu'un caractère dit homologue est bien homologue et 3) qu'un cladogramme n'est pas plus près de la vérité qu'un quelconque dendrogramme non cladistique, si l'on n'a pas, au préalable, reconnu que l'analyse cladistique est la seule procédure opérationnelle d'optimisation des homologies au sens évolutionniste du terme, c'est-à-dire des homologies qui permettent d'identifier des clades. Ces homologies là sont les « homogénies » de Lankester (1870), les synapomorphies de Hennig (1966) ou bien encore les « homologies secondaires » de De Pinna (1991). Ce sont celles qui sont situées sur un nœud précis de l'arbre et qui, par là-même, définissent un clade, ou bien qui se situent sur plusieurs nœuds d'un arbre (homoplasie) et qui définissent alors plusieurs clades. Or nombre d'auteurs ne retiennent sous le vocable « homologie » que l'« homologie primaire » des cladistes, c'est-à-dire la simple ressemblance, ou font la confusion entre homologies primaire et secondaire. On me permettra d'avancer que les biologistes des molécules ont entretenu la confusion à tel point que certains d'entre eux ont tiré un signal d'alarme afin que le terme d'homologie garde celui qu'il avait acquis lors de l'émergence de la théorie de l'évolution (Reeck *et al.*, 1987).

Toutes les méthodes de construction d'arbres partent d'une matrice de données : caractères x taxons. L'analyse cladistique traite les caractères discrets. L'homologie primaire concerne l'identification d'un caractère. S'il s'agit d'un caractère moléculaire (Fig. 1) ce peut être, par exemple, la position n° 66 dans un gène, occupée par une guanine ou une thymine. En cladistique, la transformation G → T – ou l'inverse – est assimilée à un événement évolutif. L'homologie secondaire est la présence sur un nœud précis de l'arbre d'une thymine (homologie secondaire = synapomorphie : apomorphie du groupe (Y,Z)) ou bien la présence multiple de la thymine (homoplasie qui se résoud en synapomorphies multiples de V, d'une part, et d'autre part de (Y,Z). Cette procédure d'optimisation des états du caractère 66 sur l'arbre construit à partir de tous les caractères est le fait de l'analyse dite de parcimonie qu'on pourrait dénommer, pour plus de clarté, analyse d'optimisation des homologies (Tassy & Barriel 1996). Aucune comparaison de taxons pris deux à deux avec constitution d'une matrice de distance ne fait cela : les indices de similitude ne sont pas assimilables à des événements évolutifs. Ce qui, dans l'analyse cladistique, attire les systématiciens évolutionnistes n'est donc rien d'autre que la gestion de l'homologie et, par voie de conséquence, de l'homoplasie. Dans un gène, la présence d'une thymine en position 66 chez différents taxons (V, Y et Z de la figure 1) ne dit rien ou si peu (d'un point de vue adaptatif ou biomécanique), sur la signification biologique de ce trait. Pour cette raison on a oublié, à tort, que le caractère individuel reste à la fois le lieu et le signal de l'évolution et donc le moyen de retracer la phylogénie, que le caractère soit morphologique ou moléculaire.

Un systématicien peu soupçonnable de minorer l'apport de la biologie moléculaire à la recherche phylogénétique a remarqué que les morphologistes ont largement abandonné l'usage de méthodes phénétiques, qu'elles soient de type UPGMA ou de *Neighbor Joining*, et non les biologistes des molécules (Lecointre 1994). On peut trouver différentes raisons.

L'une d'entre elles réside dans le problème de l'homologie primaire. Les morphologistes, depuis longtemps, discutent de la qualité de l'observation d'où dépend l'hypothèse d'homologie primaire. Dans bien des cas le consensus sur les caractères fait que l'homologie primaire est tenue, à tort, pour un fait d'observation. En tout état de cause les efforts principaux sont faits au niveau de l'identification des caractères. En biologie moléculaire, l'hypothèse d'homologie primaire est la conséquence de l'alignement. Comme il n'existe pas de solution optimale pour l'alignement simultané de nombreuses séquences, l'homologie primaire moléculaire, même qualifiée de statistique (Patterson, 1988), reste éminemment fragile. Un exemple est fourni par deux séquences du pseudogène éta-globine du Chimpanzé nain (*Pan paniscus*), publiées par Bailey *et al.* (1992) et par Barriel (1994a). La partie commune aux deux séquences (4919 pb), une fois alignée avec 13 séquences de Primates, présente (outre 3 nucléotides différents dans la séquence elle-même) 22 zones différentes, conséquence directe des 2 alignements effectués par Bailey *et al.* et par Barriel. Pour ces 22 zones, l'homologie primaire n'est donc pas la même et, par voie de conséquence, les homologies secondaires (synapomorphies) qui y sont liées sont distinctes (en nature et en nombre), même si l'arbre est le même.

Une autre explication tient aux simulations destinées à éprouver les méthodes de reconstruction phylogénétique, très prisées, de longue date, par les biologistes des molécules. Ces simulations ont pour but de tester l'efficacité d'une méthode par rapport à un « arbre vrai » choisi comme référence. La règle générale de ce genre d'approche est qu'une méthode a d'autant plus de chances de découvrir l'arbre vrai qu'elle incorpore les paramètres utilisés dans la simulation. De la sorte, il est facile de montrer qu'une méthode de distances peut effectivement fournir l'arbre vrai, indépendamment de la recherche des homologies. En revanche, le morphologiste est plutôt agnostique vis-à-vis d'un arbre préalable. Sa foi se porte sur la force du message donné par la seule congruence des caractères.

L'usage que l'on fait du cladogramme fournit une autre raison. Les morphologistes essaient d'identifier les caractères diagnostiques des clades afin d'émettre, dans une seconde étape, des hypothèses sur les conditions dans lesquelles sont apparus ces caractères assimilés à des événements évolutifs, autrement dit l'édification de scénarios (Deleporte, 1993). Les biologistes des molécules ne se préoccupent pas de la même manière de scénarios évolutifs et, de ce fait, ne se préoccupent guère de l'homologie secondaire ni de ce qui permet de la déceler : le cladogramme.

Les critiques de l'analyse cladistique qui ignorent la spécificité des algorithmes de parcimonie – construire un arbre en optimisant l'homologie par le traitement simultané des caractères pris individuellement – se trompent de cible. Le vrai problème des constructions d'arbres parcimonieux est le défi posé en termes de complexité algorithmique. On sait qu'au-delà de vingt-cinq taxons environ l'usage d'algorithmes heuristiques est le seul possible. Pour ceux qui souhaitent une solution exacte (ou optimale en termes d'informatique) l'approche de parcimonie souffre donc d'une faiblesse intrinsèque. Restent alors les méthodes de distance : au moyen des corrections des distances liées aux modélisations de processus évolutifs on admet alors que les clusters obtenus ont

quelque lien avec les clades issus de l'approche cladistique. Ce n'est toutefois jamais certain, même dans le cas de situations simples. On est ramené au débat sur le choix entre clusters exacts et clades heuristiques.

Vers de meilleures méthodes

Il reste la critique de Cavalli-Sforza *et al.* (1994) énoncée au début de cet article : la méthode de parcimonie n'est pas testable et n'est pas scientifique. Ce qui est visé, semble-t-il, au travers de ce jugement sans nuance est la revendication de nombreux cladistes selon laquelle la méthode de parcimonie n'est inféodée à aucun modèle évolutif. Il serait plus exact de dire que le modèle évolutif lié à l'application de la parcimonie est un modèle minimaliste, qui veut que, entre le début et la fin d'une branche, c'est-à-dire du nœud interne jusqu'au taxon terminal, la probabilité de changement d'un caractère dérivé partagé soit nulle (Darlu, 1994 ; Goujet & Tassy, 1994) ; par exemple, le partage de la thymine par les taxons Y et Z de la figure 1. C'est effectivement à cette condition que l'observation des états de caractères a une signification phylogénétique. Cela étant posé, on peut envisager nombre de situations évolutives où la parcimonie fournit une solution erronée. Mais, de la même façon, on peut envisager autant de situations où toutes les méthodes connues fournissent une solution erronée. Un exemple très simple peut être trouvé dans Darlu & Tassy (1993 : 126) avec une matrice de caractères binaires où le seul piège réside dans les quantités d'évolutions très différentes entre groupes frères. En réalité, la procédure de parcimonie n'est ni plus ni moins testable que tout autre méthode.

Pourtant ce type de critique est fréquent en biologie moléculaire. Des modèles évolutifs différents peuvent être envisagés à partir de différents cas de substitution des nucléotides. De la sorte, en phénétique, les distances sont corrigées en fonction de ces différentes situations qui peuvent être modélisées *a priori* ou bien déduites de la lecture de la matrice de données : transitions plus fréquentes que les transversions, substitutions G→C plus fréquentes etc. Ces corrections rendraient les méthodes phénétiques plus efficaces que les méthodes de parcimonie. Cette question est au cœur d'un récent débat à propos des performances et des limites de la méthode de parcimonie (Stewart, 1993, 1994 ; Sidow, 1994). C'est oublier que ces corrections sont intégrables dans les analyses de parcimonie, et, pour certaines d'entre elles (rapport transition/transversion) sont traitées automatiquement par les logiciels les plus utilisés (notamment PAUP). Cette correction qui revient à pondérer les transformations est même rendue possible par le biais d'un recodage des données ce qui permet l'usage de logiciels qui n'intègrent pas de telles options, comme Hennig86 conçu d'abord pour les données morphologiques (Wheeler & Nixon 1994). C'est d'ailleurs sur ce plan que l'on peut opposer morphologie et molécules. Modéliser les probabilités de transformations des données morphologiques n'a guère de sens. Un exemple simple à propos de l'origine de l'Homme : quel est, en soi, la probabilité de la transformation du sacrum, depuis un sacrum étroit et haut vers un sacrum bas et large ? Le partage par *Homo sapiens* et par *Australopithecus afarensis* du dernier état cité fait de ce trait, *in fine*, une synapomorphie : c'est admettre qu'à partir de l'ancêtre commun (nœud interne) il n'y a pas eu changement sur les branches terminales. C'est, en termes de processus, un modèle qui à partir de la souche commune n'implique pas de retour vers l'état plésiomorphe suivi d'une nouvelle transformation vers l'état apomorphe. Autrement dit, de l'observation du même état chez les deux Hominidés est directement tirée une hypothèse phylogénétique sans événements cachés. Nous ne savons rien des probabilités de transformation de ce genre de caractères et un tel modèle minimaliste ne choque pas les paléontologues puisque, avant tout, il faut être pragmatique. C'est ce que veulent dire Penny *et al.* (1994 : 218) lorsqu'ils affirment : « If we « don't know anything » then parsimony (minimizing changes to the data) is the best we can do for selecting the tree ». Si l'on sait autre chose, c'est-à-dire, par exemple, que les transitions sont plus fréquentes que les transversions et, par conséquent, sont susceptibles d'entraîner des homoplasies, il est alors légitime de pondérer ces transformations. Il n'est pas nécessaire pour autant de passer par des méthodes de distances. Il est vrai qu'en matière d'automatisation, face à la multiplicité des modèles évolutifs envisageables, il reste des progrès à faire (Penny *et al.* 1994). Mais, une fois encore, ces problèmes opérationnels ne sont pas étrangers à la sphère de l'analyse cladistique. Récemment, des comparaisons de situations empiriques et de simulations ont parfaitement montré dans quelles situations les méthodes cladistiques pondérées ou non pondérées donnaient de bons ou de moins bons résultats (Huelsenbeck & Hillis, 1993 ; Huelsenbeck, 1995) ; ce faisant, l'approche de parcimonie se révélait particulièrement testable, et la critique de Cavalli-Sforza *et al.* (1994) se voit réfutée.

Cependant, et très précisément, les travaux de Huelsenbeck et de Hillis que je viens de citer font écho, de façon plus détaillée, à l'article de Hillis *et al.* (1994) invoqué au début de cet article et qui a entraîné les réactions de Edwards (1995) et de Nei *et al.* (1995). Je conseille fortement la lecture des différentes facettes de ce débat et naturellement celle de la réponse de Hillis &

Huelsenbeck (1995). Qu'on me permette de faire ici succinctement de la sociologie des sciences. Le point de vue de Nei et de ses collaborateurs s'apparente à celui de Sneath et de Cavalli-Sforza : il ne peut être de meilleures méthodes que les méthodes de distances, notamment le *NJ* conçu par Nei (Saitou & Nei, 1987). De fait, le commentaire de Nei *et al.* (1995 : 253) débute par l'énoncé de la conclusion tirée par Hillis et Huelsenbeck et à laquelle Nei *et al.* ne sauraient souscrire : « when realistic conditions are considered, the maximum parsimony method is generally superior to other methods such as the neighbor joining (NJ) method and UPGMA in the recovery of a true phylogeny ». Afin de réfuter cette assertion, Nei *et al.* donnent différentes situations où la parcimonie est mise en échec. De son côté, Edwards (1995) critique globalement la sphère dans laquelle est mené ce type de recherche : les simulations numériques. Selon Edwards, le problème n'est pas tant de montrer l'adéquation d'une méthode particulière à un processus particulier que d'admettre qu'il n'est pas possible de simuler des constructions phylogénétiques sans modèle probabiliste. Dans ce cas, s'impose alors l'usage d'une méthode probabiliste, la méthode de maximum de vraisemblance, approche ni phénétique, ni cladistique. N'oublions pas que Edwards, avec Cavalli-Sforza, a introduit dans le domaine de la biologie cette méthode probabiliste tirée des travaux de Fisher (Edwards & Cavalli-Sforza, 1964). La méthode est-elle riche de promesses ? Elle cherche l'arbre le plus vraisemblable compte tenu d'un modèle évolutif donné (voir notamment Felsenstein, 1973, 1981 ; une présentation en français est donnée par Darlu & Tassy, 1993) et, naturellement, plus que les autres, elle s'approche au mieux de l'arbre vrai dans les modélisations et simulations dès lors que le modèle correspond à la réalité (Huelsenbeck, 1994). Mais la restriction actuelle de son emploi réside dans son coût en termes de temps de calcul et, de façon liée, sa limitation en termes de nombre d'espèces étudiables simultanément. C'est ce qu'ont souligné Hillis & Huelsenbeck (1995) en ajoutant que les modèles évolutifs implémentés dans les procédures de maximum de vraisemblance sont de surcroît très simples et certainement éloignés de ce qui peut se passer dans la réalité. On peut cependant espérer que dans un avenir proche l'application de la méthode du maximum de vraisemblance aux problèmes phylogénétiques permettra de construire des arbres en donnant, en termes de probabilités, les états aux nœuds : c'est-à-dire optimiser les homologies et les homoplasies. Je parie néanmoins que les modèles probabilistes les plus fréquemment utilisés seront ceux qui correspondent aujourd'hui à la parcimonie, notamment la parcimonie pondérée.

Nelson (1994) a qualifié modestement le cladisme comme une simple critique de la systématique, c'est-à-dire une critique de certaines façons de pratiquer la systématique. Même si la version informatisée de la systématique phylogénétique est un progrès considérable, il reste beaucoup à faire, y compris dans des domaines de base comme celui de l'homologie primaire. Le codage des caractères à états multiples reste une question ayant suscité différentes réponses, qu'il s'agisse de caractères morphologiques (Mickevich & Lipscomb 1991 ; Lipscomb, 1993 ; Barriel & Tassy, 1993) ou moléculaires avec notamment le problème de la gestion des insertions/délétions pour lequel une solution élégante à été récemment proposée (Barriel, 1994b). Il n'est pas question d'affirmer que les méthodes cladistiques, en l'état actuel, ne sont pas perfectibles et correspondent d'ores et déjà à l'aboutissement de la recherche phylogénétique.

Je n'ai abordé dans cet article que quelques-uns des points tournant autour du choix d'une méthode phylogénétique, en l'occurrence la méthode cladistique. L'attrait de la notion d'homologie reste le garant de la longévité des méthodes de parcimonie. C'est pourquoi rien n'annonce l'extinction du cladisme. Je me suis déjà attaché à montrer que le cladogramme est la réalisation actuelle des buts poursuivis par la systématique évolutive depuis Darwin (Tassy, 1991). Mais loin de considérer que les méthodes ont acquis leur optimum, force est de constater que des progrès restent à faire. Ces progrès seront d'autant plus fructueux qu'ils n'évacueront pas la notion d'homologie. Il est vrai que les statisticiens constructeurs d'arbres n'aiment pas ce concept d'homologie, concept apparemment plus intuitif que statistique. C'est précisément pourquoi certains d'entre eux, à la fin des années cinquante s'étaient attachés à concevoir des méthodes automatiques non phylogénétiques. Après tout, la phylogénie est une histoire, le fruit de la contingence. Il ne faut pas s'étonner que la plupart des tests statistiques en matière de robustesse d'arbres (*bootstrap* et autre *jackknife*) ont des résultats particulièrement sévères : peu de clades se révèlent statistiquement robustes. Je n'aborderai pas ici la question du lien entre l'arbre de *bootstrap* et l'arbre phylogénétique. On peut se poser une question, en manière de provocation : est-on sûr qu'un événement évolutif – définissant nécessairement un clade – qui a eu lieu à un quelconque moment dans le passé puisse, à tout coup, se révéler robuste au moyen de méthodes statistiques, même s'il se trouve là, quelque part dans la matrice de données ? L'exemple cité plus haut (Darlu & Tassy,1993 : 126, 131) d'une matrice simple mettant en échec les différentes méthodes de reconstruction phylogénétique fournit une belle illustration de ce paradoxe. L'arbre de *bootstrap* (*majority rule consensus*) obtenu par parcimonie après cent ré-échantillonnages fournit 10 des 11 « vrais » clades mais 5 de ces clades ont des valeurs inférieures à 80 de telle sorte que

l'on devrait en déduire qu'ils sont statistiquement non fondés. Tel est le casse-tête de la construction phylogénétique. Tout est de l'ordre de l'hypothèse, fragile, depuis l'homologie primaire jusqu'à l'établissement de l'arbre et l'identification des clades et de leurs traits associés ; au moins pouvons-nous, aujourd'hui, mesurer cette fragilité. Hennig (1966 : 94) d'ailleurs n'a jamais rien dit d'autre dans sa définition de l'homologie (« in determining homologies we are limited to erecting hypotheses »).

En guise de conclusion, je répéterai un mot de Claude Bernard que j'ai déjà cité il y a 14 ans à propos de cladisme, avant d'avoir jamais manipulé un quelconque logiciel de parcimonie, mais qui s'applique toujours merveilleusement à la recherche phylogénétique : « Quand nous faisons une théorie générale dans nos sciences, la seule chose dont nous soyons certains, c'est que toutes ces théories sont fausses absolument parlant. Elles ne sont que des vérités partielles et provisoires qui nous sont nécessaires (...) pour avancer l'investigation » (Bernard 1865 : 63).

REMERCIEMENTS – L'aide de Véronique Barriel et de Pierre Darlu, comme toujours, m'a été extrêmement profitable. Merci également à Guillaume Lecointre pour ses commentaires et suggestions, notamment à propos des « arbres vrais ». Néanmoins, selon la formule consacrée, j'assume la responsabilité des erreurs dues à mes partis pris.

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Reçu le 15 janvier 1996; received January 15, 1996
Accepté le 8 mars 1996; accepted March 8, 1996

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VIE MILIEU, 1996, 46 (2) : 125-138

FIRST PRINCIPLES OF PHYLOGENETIC SYSTEMATICS, A BASIS FOR NUMERICAL METHODS USED FOR MORPHOLOGICAL AND MOLECULAR CHARACTERS

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MOLECULAR SYSTEMATICS
PHYLOGENETIC SYSTEMATICS
rDNA
CLADISTICS
ARTHROPODA
CRUSTACEA

SUMMARY. – Principles that are the basis of phylogenetic systematics should be independent of the type of characters used. Established numerical methods for phylogeny inference have produced many controversial results, their reliability is questioned. Character classes are discussed to stress that the phylogenetic signal is identical with Hennig's concept of apomorphy. Homology is defined such that the term can be used in molecular systematics as well as in comparative morphology. The importance of pattern recognition without the use of models, the concept of the information content of characters, of probability of homology, and the term "phenetic cladistics" are explained. Spectra of apomorphies are proposed as new tools for the *a priori* character analysis of aligned sequences. It is shown that 18SrDNA sequences conserve little information on early arthropod radiation.

SYSTÉMATIQUE MOLÉCULAIRE
SYSTÉMATIQUE PHYLOGÉNÉTIQUE
ADNr
CLADISTIQUE
ARTHROPODA
CRUSTACEA

RÉSUMÉ. – Les principes de base de la systématique phylogénétique devraient être indépendants du type de caractères utilisés. Les méthodes numériques établies en vue de l'inférence phylogénétique ont donné des résultats sujets à controverse ; leur fiabilité est évaluée de manière critique. Les classes de caractères sont discutées afin de souligner que le signal phylogénétique est identique au concept d'apomorphie de Hennig. L'homologie est définie de façon à ce que le terme puisse être utilisé en systématique moléculaire et en morphologie comparative. L'importance de la reconnaissance du pattern sans utiliser de modèles, le concept du contenu en information des caractères, de probabilité de l'homologie, et le terme "cladistique phénétique" sont expliqués. Des spectres d'apomorphies sont proposés en tant que nouveaux outils dans l'analyse *a priori* des caractères d'alignements de séquences. Les séquences d'ADNr 18S conservent peu d'information sur la radiation précoce des arthropodes.

1. INTRODUCTION

Assuming that the established methods of phylogeny inference are reliable, dendrograms for the same taxa based on different data sets should reflect the same history of phylogenesis. In practice, this is not the case. Today, one can choose among many incompatible tree topologies, most of these presented by their authors as putative real phylogenies. Very often taxa of metazoans, for which very informative apomorphies (e.g. complex morphological characters) are known, appear to be para- or polyphyletic when sequence data are used. Some examples visualize this problem :

— Lake 1990 (using 18S rRNA and evolutionary parsimony) : arthropods are polyphyletic. Wheeler *et al.* 1993 (morphological and molecular data, maximum parsimony) : arthropods are monophyletic ;

— Hendriks *et al.* 1988 (18S rRNA and distance methods) : Mandibulata are paraphyletic ; Ballard *et al.* 1992 (12Sr RNA, maximum parsimony and neighbor joining) and Friedrich & Tautz 1995 (rDNA and various tree-constructing methods) : Mandibulata are polyphyletic ; Boore *et al.* 1995 (mtDNA rearrangements) : Mandibulata are monophyletic ;

— Kim & Bae 1992 (18S rRNA, UPGMA and maximum parsimony) : Brachyura are paraphyletic ; Spears *et al.* 1992 (18S rRNA and maximum parsimony) : Brachyura are monophyletic ;

— Katayama *et al.* 1993 (18S rDNA, neighbor joining) : Plathelminthes are paraphyletic ;

— Kobayashi *et al.* 1993 (18S rDNA, neighbor joining) : Porifera are paraphyletic ;

— Kojima *et al.* 1993 (EF-1 alpha, maximum likelihood) : Articulata are polyphyletic ;

— Friedrich & Tautz 1995 (rDNA, various tree-constructing methods) : Tracheata are polyphyletic; — Pettigrew *et al.* 1989 (haemoglobin sequence, clustering and maximum likelihood) : Chiroptera are polyphyletic; Baker *et al.* 1991 (morphological characters) : Chiroptera are monophyletic.

Simultaneously, there exist disagreements between morphologists, which use different methods for tree construction or for interpretation of characters. It appears that two major causes are responsible for these disagreements : a) data sets may differ in their information content, b) tree construction methods differ in their implicit ability to discern between the phylogenetic signal (apomorphies) and irrelevant information (noise, trivial characters, analogies, plesiomorphies).

The present paper is dedicated to the search of first principles that should constitute the basis of a synthetic theory of systematics. Several of the statements found in this paper will be familiar to morphologists, other aspects may be trivial from the point of view of a molecular systematist. I learned in many discussions that what seems to be common knowledge to one scientist, has never been heard of by another one who has a different background. Because communication is often difficult when terms are defined in various ways by different schools, it is intended to explicitely exclude ambiguity in the central terms used in the following.

2. METHODS

The methodology of phylogenetic systematics sensu Hennig has been described very often, though with varying precision (Hennig 1950, 1966, 1982, Wiley 1981, Ax 1988, Sudhaus & Rehfeld 1992). It is not identical with "cladistics", as will be explained in the following paragraphs. Numerical methods are described in many of the publications cited in manuals for the computer programs mentioned below (see also a review in Swofford & Olsen 1990). For reanalysis of sequence data, the following computer programs were used : PAUP (Swofford 1991), MEGA (Kumar *et al.* 1993), DNAML (Felsenstein 1993), CLUSTALV (Higgins & Sharp 1988), MALIGN (Wheeler & Gladstein 1994), SPLITSTREE (Huson & Wetzel 1994), ENCOMP (G. Stanjek, unpublished). Information content of sequence data was estimated using ideas of the author (Wägele 1995, Wägele in press, and unpublished information). The procedure is briefly explained in Chapter 11. For the example of Chapter 12, mainly sequences published in the following references were used : Hendriks *et al.* 1988, Abele *et al.* 1989, Kim & Abele 1990, Kim *et al.* 1993, Spears *et al.* 1994. Further sequences (with genbank ID number) : *Artemia salina* (X01723), *Daphnia galeata* (Z23111), *Stenocypris major* (Z22850), *Panulirus argus* (U19182), *Androctonus australis* (X77908), *Glycera americana* (U19519).

3. WHICH EVIDENCE CAN BE USED FOR INFERENCE OF PHYLOGENY ?

The answer to this question is part of the strict logical theory of systematics developed (or discovered) by W. Hennig (1950). While (hopefully) many morphologists are familiar with Hennigs discoveries, many molecular systematists tend to ignore or to reject the Hennigian methodology. The most important laws of the latter are :

(a) superficial similarity is no evidence for close relationship, (b) similarity based on inheritance of the same genetic information (i.e. homology) is not necessarily evidence for a sistergroup-relationship, and (c) new information that appears for the first time in the last common ancestor of a group of taxa is the phylogenetic signal (apomorphies) that must be identified in descendants to support a hypothesis of monophyly.

For (a), it must be remembered that superficial similarity is often the result of analogy or of convergent evolution. For (b), it is important to realize that phylogenetically old information (plesiomorphies) is often conserved in distantly related taxa (e.g. egg-laying in snakes and crocodiles). These laws are a direct consequence of the theory of evolution : genetic information that survives selection and genetic drift, is inherited by descendants.

4. WHICH CLASSES OF SIMILARITIES (CHARACTERS) CAN BE DISTINGUISHED ?

Classification of characters according to the phylogenetic information they bear (see also Hennig 1950, 1966) :

— ***Autapomorphies*** (= ***trivial characters***) : new characters that appear for the first time in a ***single*** species or in a ***single*** terminal taxon. Autapomorphies are trivial because they are not parsimony-informative.

— ***Apomorphies*** : new characters inherited by ***several*** organisms from a last common ancestor. This is the phylogenetic signal we must search for. ***Synapomorphies*** occur in sistergroups (i.e. exactly in ***two*** taxa; see also the strict definition in Ax 1988, 1995).

— ***Plesiomorphies*** : characters that are inherited from an ancestor older than the last common ancestor and which therefore may be present in outgroup taxa.
— ***Analogies*** : superficial similarities not based on shared apomorphies ("false signal").

In addition to these four classes, we find – particularly in sequences – ***noise*** : variations that may show similarities but do not allow unambiguous classification; typical for features evolving fast or that change with very few mutations.

The ***apomorphy*** defined as "new character" is strict logically not the same as the ***apomorphic character state***, though in practice this distinction is not made by morphologists. The latter expression can be applied to a conserved pattern (a homology), which frames a new detail (an added piece of information, a substitution s.l.). This new detail is the apomorphy s.str.. The ambiguous use of the term apomorphy does not occur in sequence analysis, where substitutions and conserved nucleotides can easily be distinguished in a given alignment.

5. WHAT IS A HOMOLOGY?

The term homology has been omitted in the previous paragraph, because usually it is a complex pattern composed of several classes of characters. Definitions of the term, including that of Hennig (1966 : 93), usually do not discern between classes of similarities. Van Valen's (1982) definition for example ("correspondence caused by continuity of information") is too fuzzy : the correspondence does not exclude that some dissimilarities are present. This sometimes has odd consequences. Wiley *et al.* (1991, p. 9) for example write :

"An evolutionary novelty is an inherited change from a previously existing character. The **novelty is the homologue** of the previously existing character in an ancestor/descendant relationship."

The term "novelty" could refer to a complex homology that frames a substitution. However, the statement also implies that an autapomorphy s.str. (new genetic information in a descendant, a substition s.l.), which was not present in the ancestor, is a homology. This concept, though familiar to morphologists, is not acceptable when sequences are compared. How can a new and unique character be homologous with the absence of this specific information in the ancestor or in a related organism (that does not bear this novelty)? If one wishes to find a common basis for comparative morphology and sequence analysis, homology has to be defined in a more precise way, ***excluding autapomorphies*** (see also Dohle 1989), for example as follows :

"A homology is genetic information, or the expression of this information, which has been inherited from the last common ancestor of those organisms that possess this information."

Therefore, a homology is usually composed of shared apomorphies and plesiomorphies, but autapomorphies of terminal taxa (noted as dissimilarities) must be excluded, because they were not inherited from the last common ancestor. If shared apomorphies are not present in a pattern, the homology is composed of plesiomorphies (e.g. "mammalian hair" in primates); if only a single shared apomorphy is described, it also is a homology.

Of course, this definition of homology implies that synapomorphy and homology are not the same. The latter conception (e.g. Patterson 1982, Nelson 1994) is only correct when read in one direction : a synapomorphy is a homology. However, it is common practice to use the term homology also in a wider sense, namely for complex characters that also contain symplesiomophic details, or that are plesiomorphies (character "mamalian hair" in primates). Therefore, ***a homology is not always a synapomorphy***.

A complex morphological character usually is a pattern with conserved details discernible in several organisms. The conserved details (the frame) allow identification of single modifications (novelties) within the pattern. Riedl (1975) named the details "***minimum homologies***" occurring within a "***frame homology***". This is equivalent to a conserved sequence position in a gene. The largest homology is the complete bauplan (in the sense of all shared information that had been present in the last common ancestor) of a group of organisms (Wägele 1995). The ***frame homology*** is a functional or structural unit which our brain is able to discern from other such units (we are still dependent of our innate and trained cognitive abilities). The simplest homology we know is the nucleotide in a sequence position. The latter can only be identified within a frame of conserved positions.

It is not fruitful to discuss here all major contributions dealing with the term homology (reviews e.g. in Rieppel 1992, Minelli 1993, Hall 1994). Differences between concepts are important because they have practical consequences : a problem arises when systematists do not care about character analysis prior to a cladistic analysis. These persons use the criterion of congruence (in the sense of Patterson 1982, 1988) and hope that character distribution on a tree will discriminate analogies and homologies. However, as discussed below, "phylogeny is not... the criterion for testing hypotheses about homologous features" (Bock

1989 : 335). In short, a single similarity is not an apomorphy just because it fits to a given most parsimonious tree topology (the opposite view is defended e.g. by Nelson 1994).

6. FACTS AND HYPOTHESES

A similarity can be identified intersubjectively relying on our sense organs or on some measurement and therefore could be accepted as a "fact". However, the interpretation of a similarity as a product of an evolutionary process is always a hypothesis, no matter how the analysis was carried out. After recognition of similarity, the systematist has to discern between hypotheses of analogy versus hypotheses of homology. A morphologist usually also discerns between "good characters", i.e. characters where homology is very probable, and "weak characters", where homology is doubtful. This is equivalent to the difference between unambiguous areas in multiple alignments and sequence parts of doubtful alignment. In practice, "good characters" are usually complex or embedded in complex, conserved surroundings, indicating the presence of a large amount of specific, identical genetic information. The probability that such a similarity evolves by chance or by convergence is inversely proportional to the information content (specific complexity, see below) of the character. **Probability of homology** is higher when a larger number of specific mutations may be the cause for a morphological apomorphy, or when a rare (improbable) event like a specific inversion causes a molecular apomorphy. The "criteria for homology" of Remane (1961) are criteria to estimate information content or probability (Riedl 1975).

At this point, it might be necessary to present a concept on what ***"information"*** means in systematics : characters can be regarded to be patterns. The information we need is the probability that a pattern seen in several individuals evolved only once. This problem is related to the concept of information in **cybernetics** : the probability that a pattern observed more than once has a single source (e.g. a sound heard in two radios) depends on the complexity of the pattern and on the number of possible alternatives (Shannon 1948). The principle of parsimony must be applied to character analysis, too : the most parsimonious explanation for the occurrence of many identities in two patterns is that there is a common source of information. Thus, the selection of "good characters" does not stand on an *a priori* model of evolutionary processes. Using a phenomenological approach, a systematist can not calculate this probability precisely, but nevertheless it is possible to discern between more complex characters and simpler (risky) ones. A specific statocyst construction is more informative than a polymorphic pigment pattern; a complete gene usually bears more data than a few base pairs. An experienced taxonomist is able to discern between very variable (noisy) characters and more stable ones, where obviously the probability that mutations will change the pattern is low. The fact that a simple feature (e.g. a bristle at a specific location) can be highly conserved and therefore is used by taxonomists, is no counter-example : the taxonomist in reality is using the complete pattern, i.e. the bristle with its surroundings, to identify the character; the pattern is more complex than explicitly stated.

A referee asked : how can we discern that a homology is probable without making a tree? Well, a tree of the Amniota is not needed to state that a feather is with high probability a homology in all species that have a plumage. This is equivalent to say that with high probability a sound you here simultaneously in two radios (e.g. an unintelligible chinese sentence) has a single source.

7. PATTERNS AND PROCESSES, NULL MODELS, RECOGNITION AND EXPLANATION

Similarity of a complex pattern visible in different objects is detected by our brain by an usually unconscious mechanism without the need of assumptions about processes that produced these patterns. Thus, a child without scientific education is able to classify animals into "birds", "dogs", "turtles". Analysis of patterns ***without assumptions about processes*** is possible in phylogenetic systematics sensu Hennig and in phenetic cladistics. However, pattern analysis in a phylogenetic study will only be successful, when it aims at a discrimination between phylogenetic signal, false signal and noise, i.e. ***when part of the available characters is discarded***. Otherwise, the result of a cladistic analysis will depend entirely on the numerical proportion between different classes of similarities. This obviously leads to errors. Here we find the foundation for an important difference between the Hennigian methodology and phenetic cladistics (see Chapter 13).

When distance and maximum likelihood methods are used, character analysis is not striven for. To neutralize the effect of noise caused by trivial characters and of plesiomorphies, assumptions about the historical process of substitutions in stem-lineages of extant taxa are necessary. To assume processes using models of nucleotide

substitutions in sequence analysis (e.g. Tajima & Nei 1984, Gojobori *et al.* 1990, Rodríguez *et al.* 1990, Li & Graur 1991, Yang *et al.* 1994) implies that part of the ***explanation*** (for the existence of specific patterns) is influencing pattern ***recognition***. Thus, studying the reliability of tree-constructing algorithms with simulations of sequence evolution (e.g. Felsenstein 1988, Li & Gouy 1991, Zharkikh & Li 1993), usually it will be that algorithm that considers the model used for the simulation which gives the best result (e.g. Hillis *et al.* 1993). In other words, to make strong assumptions about sequence evolution and to use these for pattern recognition procedures may lead to circular reasoning. This problem, together with the fact that character analysis is missing, is one reason why distance or likelihood methods are not more trustworthy than e.g. maximum parsimony.

To assume that sequences evolve according to some stochastic process is an attempt to introduce an explanation into pattern recognition. This assumption violates the observations and laws well known by those biologists that study the evolution of populations. Even when assuming that mutations are neutral and their appearance is stochastic, the rate at which they are fixed depends on changes of population size (Maynard Smith 1989). Since morphologists observe evidence for "sudden" bursts of evolutionary change, these must also be expected in the genome (e.g. Britten 1986, Carpenter 1990, Lewin 1990). Besides expected phenomena such as the influence of body size or metabolic rate on substitution rates (e.g. Martin & Palumbi 1993, Adachi *et al.* 1993) other effects are unpredictable. Fixation of a mutation in a population (= substitution s.l.) depends on the fit of the character function to an ecological niche (e.g. Riedl 1975), an effect that cannot be reconstructed in enough detail to allow calculation of genetic drift in a historical population, and fixation depends on unpredictable events such as chance survival of a few genotypes after population breakdown or chance dispersal by a storm, followed by fast adaptive radiation. It therefore must be expected that only in special cases (closely related species) sequence evolution really can be described with a model of stochastic sequence evolution. But even related species living in different habitats may show surprising variations in substitution rates (e.g. Sturmbauer & Meyer 1992). In fact, assuming that the models are useful, why then are the results so contradictory (see chapter 1)? It is obviously better to study patterns and to search for explanations *a posteriori*.

Which assumptions are necessary to analyze patterns? As already stated, to recognize simple similarity, assumptions are not necessary. To discriminate between analogy and homology, and between plesiomorphies and apomorphies, we must accept that evolution is a fact and has a polarity along time axis; that genetic information is inherited; that a large number of identities seen in two individuals indicates the existence of a late common ancestor. If we find a complex pattern repeatedly (act of ***recognition***) in different organisms, we must assume according to information theory or following the principle of parsimony (as discussed in Riedl 1975) that some process produces this pattern (act of ***explanation***), but recognition does not require knowledge of the historical process. In fact, for most morphological characters that are considered to be "good" homologies, nothing is known about the evolutionary process (When? How fast? How many mutations? Effect on fitness? Effect of population size? In which sequential order? etc... This is familiar to morphologists, but obviously not to many molecular systematists). In Chapter 11), it is shown that patterns of DNA sequences can also be studied with a phenomenological approach.

Very often it is argued that we must consider the ***function*** of characters and the ***independence*** of characters to estimate the probability of homology (or the "weight" of a character; see e.g. the weighting criteria "unaffected by ecological shifts" or "narrow specialization" in Wheeler 1986 and the distinction between paired and unpaired bases of rRNA in Wheeler & Honeycutt 1988). These arguments do not discern between ***recognition*** and ***explanation***. ***Probability of homology*** depends on the complexity of the pattern, not on its function: apparently non-functional patterns (e.g. parts of spacer sequences) will nevertheless show similarity caused by common descendance; they tend to become noisy faster than other sequences, but what we see is the noise, not the function. [Function in a different sense (muscle contraction, behavior) of course can indicate the existence of homologies; it must be shown that similar patterns (e.g. of movement) have a shared genetic cause.]

Though our brain often works out nearly simultaneously recognition of patterns and explanations for the similarity, it is important to discern consciously between these mechanisms. Function may be responsible for the conservation of patterns. The ***act of recognition*** is the observation that a pattern does not change. The analysis of the role of the pattern gives the ***explanation***. For example, it might be assumed that nucleotides in helical areas of secondary structure of RNA molecules are more conserved than single nucleotides in loops, because in the latter the nucleotides are not paired. This, however, is no general rule. Alignments of metazoan rRNA show a different pattern: some loops are highly conserved while some helices are so variable that a reliable alignment is not possible. So, pattern recognition *precedes* the search for an explanation.

Does analysis of ***independence of characters*** contribute to the estimation of probability of homology? First of all one must ask what "independence" means. As long as characters occur together in a single individual, all characters depend on the ability of this singular organism to survive and to reproduce. A neutral mutation in a DNA sequence will not be transmitted when a genetic muscle disease disables its carrier. "Independence" could be important in another sense, namely to ensure that a single event (e.g. an inversion) should not be counted twice. But, if this event is a rare one, it would be useful to count it twice, because this is equivalent with the assignment of a higher weight. So, the question is not that of independence, but that of probability.

An example illustrates this problem. When several characters are involved in a single function, as the components of the mammalian ear, should they be coded as a single character (instead of discerning between external meatus, middle ear cavity, features of the tympanum, malleus, etc.) or should they get a lower weight, because they are not independent? Certainly not, because probability of homology is very high due to the high complexity of the complete pattern, which can be expressed by high weight or by using structural details as separate characters, thus increasing the number of apomorphies listed in the data matrix. Again, the identification of pattern complexity is important, not function or dependence.

At this point it might be useful to consider "weighting". It is not correct to state that "weighting by systematists is an *a posteriori* exercise, designed to prefer one group to another" (Patterson 1982). This is a concept typical of phenetic cladistics (see below), that leads to circular argumentation: the character that fits on a topology gets a higher weight and therefore stabilizes the topology. Successive weighting (Farris 1969) is an equivalent circular procedure. In contrast, iterative analysis (testing the plausibility to discover mistakes in character analysis: Fig. 1 in Wägele 1994) is not circular. Weighting is only an acceptable (and necessary) tool when it is used to estimate probability of homology *a priori*.

Estimation of probability of homology is the most difficult part of a phylogenetic analysis, especially when morphological characters are used, whose information content can not be quantified at the present state of the art (though a relative order of probabilities can often easily be estimated). Nevertheless, problems with practical applications are no arguments against the theory.

In general, I agree with Patterson (1994) that models should be avoided in phylogenetic systematics, observation of patterns has logical precedence over process explanations (Rieppel 1992).

8. CONGRUENCE AND PROBABILITY OF HOMOLOGY

Patterson (1988) writes: "..the most decisive test of homology is by congruence with other homologies". Congruence in the sense of "shared similarities" could mean that many details form a similar complex pattern in two species. But, congruence is defined by Patterson as compatible distribution of characters on a tree topology. Thus, the congruence test of Patterson (1982) is an *a posteriori* – test, typical for cladists that avoid *a priori* character analysis, a concept that also dominates in molecular systematics (e.g. Williams 1992). This procedure implies that all characters can be used for a cladistic analysis without consideration of their information content.

In a phenetic cladistic analysis of this type (see Chapter 10), the result depends on the overall similarity of OTU characters, the latter being selected without consideration of character class and of probability of homology. If in such a data set the phylogenetic signal is weak, there is always the danger that (false) sistergroups are supported by plesiomorphies or chance similarities (analogies) and also by the effect of trivial characters, whenever they outnumber the apomorphies (Wägele 1994). Chance similarities present in DNA sequences and producing stable but false dichotomies are discussed in an example presented in Chapter 12.

A combination of a single apomorphy of high quality (high probability of homology) with many low quality characters in a single data set will often result in calculation of a wrong topology. The congruence test sensu Patterson will then define homology for all weak characters that by chance fit to the topology, while the important character will be "drowned".

The ideas discussed previously allow one to identify a different type of congruence that indicates probability of homology: the fit of details into a complex character, which may be called "***character pattern congruence***" in contrast to "***tree topology congruence***". If a putative homology always appears in the same place of a more complex homology ("frame homology"), this detail is congruent with other details (e.g. position of an artery on a mammalian heart). This is exactly the "criterion of similarity" and at the same time the "criterion of position" as defined by Remane (1961). In molecular systematics these criteria are used in sequence alignment, which obviously is an *a priori* procedure.

9. IS THE STUDY OF THE INFORMATION CONTENT OF CHARACTERS RELEVANT?

A positive answer can be deduced from what has been said in the previous chapters. The question is important because virtually all available computer programs used for "tree construction" allow phylogenetic analysis on the basis of simple data matrices whithout test of character quality, while few numerical methods have been developed for *a priori* distinction of character classes and character information content.

Is such a test necessary? Studying published literature, many examples can be found for the misleading effects of low-quality characters. A case study for morphological characters has been discussed extensively by Wägele (1994). Gauthier *et al.* (1988), discussing the "Haemothermia" concept (Gardiner 1982), enumerate Gardiner's simplistic character descriptions of which, at close inspection, many with high probability prove to describe non-homologies. An analysis of crustacean relationships (Wilson 1992) using PAUP produced a peculiar result because, as acknowledged by the author, character analysis was missing. Characters like "sperm flagellate (0) or modified (1)", "furcal rami present (0) or absent (1)" etc. are too simple, will tend to be homoplasious and weaken the cladistic analysis. The in parts exotic cladogram of metazoans calculated by Eernisse *et al.* (1992) is also based on many weak characters or character descriptions, such as "hermaphroditic sexual system" (with no details!), "filiform morphology of sperm", "U-shaped alimentary tract", features that in this simplicity do not allow determination of homology. Baker *et al.* (1991) discuss bat monophyly and explain that the "wing index" calculated by Pettigrew *et al.* (1991) to support separation of micro- and megachiropterans is a simple number, the neuronal characters (e.g. size ratios) are weak and carelessly scored characters, while many other complex details, several not associated with flight, support monophyly.

These examples illustrate that inference of phylogeny with morphological characters requires *a priori* estimation of character class (in the sense discussed in Chapter 4 and character quality, also when computer programs are used to construct trees (e.g. Farris 1982, Stewart 1993). Is this procedure also necessary and feasible when *sequences* are used? Principally, there should be no basic differences between analyses of any type of data sets. The problem is that, until now, methods for the *a priori* search of apomorphies in sequences do not exist (or are not established). To some extent, character analysis is already good practice in sequence analysis, namely during sequence alignment. However, homology occurs on at least two different levels:

a) homology of sequence position (discovered with alignment procedures, and

b) homology of apomorphic characters states (single nucleotides).

Both determine tree topology. The effects of a) can easily be demonstrated (e.g. in Wägele & Stanjek 1995), but until now no method existed to estimate *a priori* b). A new approach will be presented in Chapter 11.

10. WHAT IS A "PHENETIC METHOD"?

In comparative morphology, a phenetic method compares phenotypic similarities without consideration of character class. Phenetic methods are therefore avoided in phylogenetic systematics. A cladistic analysis carried out without selection or weighting of characters according to probability of homology, depends on overall similarity of the species, even when a parsimony algorithm is used for tree construction, and is therefore a phenetic analysis (see Chapter 13).

Why are phenetic methods less reliable than phylogenetic ones? Phenetic methods allow that character classes other than apomorphies determine tree topology. The above-mentioned "fishes" or "reptiles" are similar due to plesiomorphies, "worms" share analogies (shape of the body). These examples are trivial, but the same pitfalls also occur in less obvious cases (Wägele 1994).

However, when the number of characters is very high (as in DNA-DNA hybridization) and several outgroups are considered, there is a good chance that a phenetic approach will find sistergroups, because character classes other than synapomorphies will (hopefully) have no effect. With a lower number of characters or absence of suitable outgroups, analogies and plesiomorphies can give a false signal.

In sequence analysis, distance methods obviously are phenetic methods. Any variable position influences the distances between terminal taxa. The following groupings of character classes occur in sequence comparison:

Positions 1 to 5 influence distance calculations, but only position 1 is a "phylogenetic signal". Position 2 is a "false signal" (analogy), destroying the effect of position 1. Positions 1 and 2 are parsimony-informative in case the root of the tree is known. Positions 3 to 5 allow no definition of groups and therefore are "trivial", but they nevertheless increase distance between sequences 1 and 2. The numerical abundance of these character classes determines whether the distance method

Table I. – Distribution of character classes influencing genetic distances for the tree ((1, 2) 3).

Position	Sequence 1	Sequence 2	Sequence 3
1	synapomorphy	synapomorphy	plesiomorphy
2	analogy	plesiomorphy	analogy
3	autapomorphy	plesiomorphy	plesiomorphy
4	autapomorphy 1	plesiomorphy	autapomorphy 2
5	autapomorphy 1	autapomorphy 2	autapomorphy 3
6	plesiomorphy	plesiomorphy	plesiomorphy

will find the correct tree or not, when Hamming distances are used. That trivial characters really influence tree topology can easily be shown (Wägele, in press). It may be hoped that using the correct model for sequence evolution the effect of analogies and autapomorphies will be corrected, but there is no guarantee. I have recently heard the following statement during a workshop : "There is empirical evidence that distance methods can identify the correct tree topology". This reminds me of the proud father telling that his little boy has driven the Cadillac into the garage without damaging it. Is this enough empirical evidence to entrust little boys a driver's licence ?

Maximum parsimony analysis excludes implicitely trivial characters, but depends on the numerical abundance of apomorphies vs. analogies. Only combined with an *a priori* search of reliable apomorphies, maximum parsimony is equivalent to the Hennigian methodology.

11. CHARACTER ANALYSIS AND IDENTIFICATION OF APOMORPHIES IN SEQUENCE DATA

Software for the *a priori* search of apomorphies in aligned sequences is being developed (program ENCOMP and new subroutines of SplitsTree) on the basis of the procedure described below. It has been tested with published sequence data sets and clearly identifies *a priori* those groups of taxa that are based on weak evidence.

The basic principle is that of probability of homology in complex patterns ("character-pattern congruence") of those nucleotides that show an apomorphy-like distribution. Two questions are intimately linked :
— probability of homology of apomorphy-like characters, and
— probability of monophyly of the group bearing the putative apomorphy.

A hypothesis of apomorphy of a character implies a hypothesis of monophyly. A single character of 100 % probability would be enough to prove monophyly of a group. Characters for which we can suppose a very high probability of apomorphy are for example the radula of molluscs or the feather of birds. Similar complex patterns should also be present in DNA sequences. To find putative apomorphies, the patterns are analyzed without reference to a model of sequence evolution :

1) Select two or more sequences from a multiple alignment at random or select a group of taxa that shall be tested. Define the selected group as *functional ingroup*. All remaining sequences form the functional outgroup (ideally as many as possible). Any combination of sequences can be tested as functional ingroup.

Steps 2) to 7) are repeated for each ingroup/outgroup-split.

2) Search for binary positions with a single nucleotide in the functional ingroup, another nucleotide in the outgroup. These positions are called *symmetrical split-supporting positions* (symmetrical because there is only one "colour" at each side of the split), they support the ingroup/outgroup-split.

3) Search for *asymmetrical split-supporting positions*, i.e. positions with a conserved single nucleotide in the ingroup, different nucleotides in the outgroup.

4) Search for further asymmetrical positions allowing some deviations ("noise"), which occur with higher probability when the number of sequences increases. Deviations are : a) *substitutions* within the ingroup (deviations from the ingroup's groundpattern), and b) *analogies* (convergencies) within the outgroup. Allow increase of number of deviations until some threshold (limit of uncertainty) is reached. The threshold should be a deviation from a random distribution of the noise. (Still not programmed for ENCOMP. For the example in Chapter 12 up to 10 % deviations per position were allowed.)

5) Add all positions found in steps 1 to 4 and define them as "ingroup supporting positions".

6) Repeat steps 1 to 5 for the alternative hypothesis of outgroup monophyly, using now the functional outgroup as functional ingroup.

7) Compare the number of supporting positions for the hypothesis of ingroup monophyly and the hypothesis of outgroup monophyly. The hypothe-

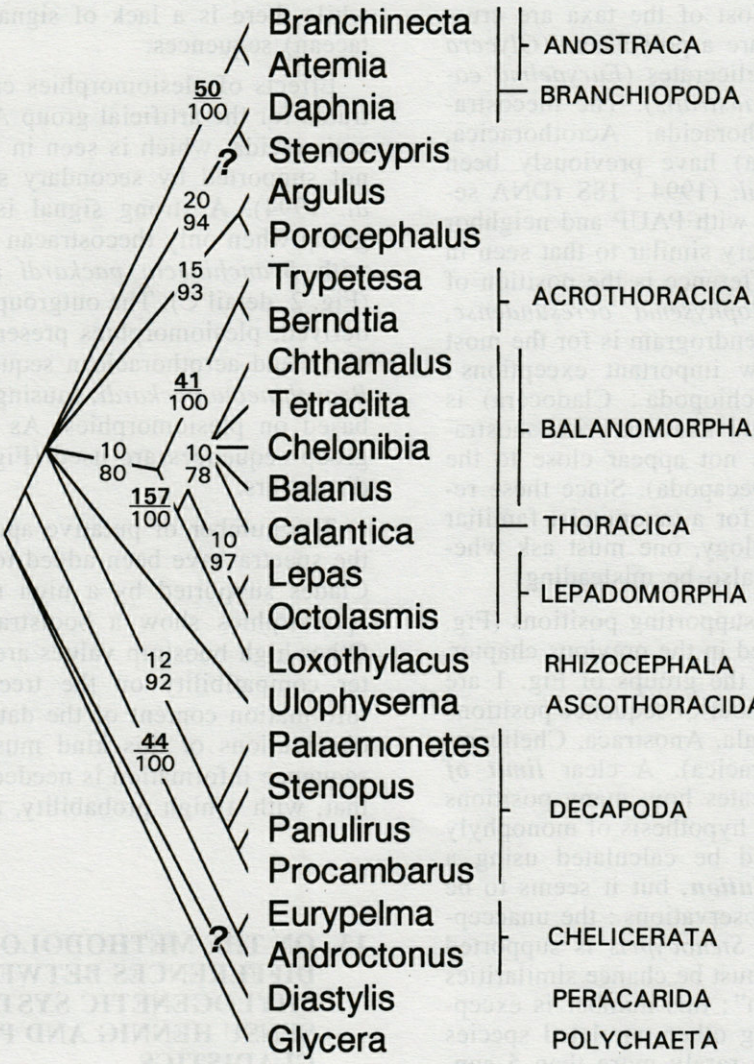


Fig. 1. – 70 % majority-rule consensus tree based on 500 maximum parsimony bootstrap replicates using PAUP. The data are 18SrDNA sequences of crustaceans (see material & methods), the sequences of *Glycera americana*, *Eurypelma californica* and *Androctonus australis* were used as outgroup data. On some important inner branches the number of putative apomorphies and the bootstrap value (below) are shown. Note that high numbers of apomorphies (bold numbers) correlate with a bootstrap value of 100 %.

sis supported by the higher number of asymmetric positions is with higher probability correct. This group will be called in the following the *putative monophylum*, the corresponding supporting positions are *putative apomorphies*.

8) To draw an "apomorphy spectrum" (Fig. 2B), substract from the supporting positions of the putative outgroup all those positions, that are also supporting monophyly of the putative ingroup. The horizontal line in Fig. 2 represents the splits, the height of the columns the number of supporting positions.

The hight of the column in Fig. 2B is a measure of the phylogenetic signal (putative apomorphies) conserved in this set of sequences. Taxa for which no distinct signal is detected are either non-monophyletic or have no conserved apomorphies. Phylogenetic analysis for such taxa is therefore risky : even if one obtains good bootstrap values, the tree topology may be incorrect. Taxa for which a high signal is found are only supported by putative apomorphies when suitable outgroup taxa (not too distant from the monophylum) are present in the data set. Otherwise, the signal could be composed of plesiomorphies, especially in groups that branch off early.

12. IDENTIFICATION OF APOMORPHIES IN SEQUENCES : EXAMPLE

Fig. 1 shows a 70 % majority-rule consensus maximum parsimony tree of 500 bootstrap replicates, calculated with PAUP for a set of 25

18SrDNA sequences. Most of the taxa are crustaceans, outgroup taxa are a polychaete (*Glycera americana*) and two chelicerates (*Eurypelma californica, Androctonus australis*). The thecostracan sequences (Ascothoracida, Acrothoracica, Rhizocephala, Thoracica) have previously been analyzed by Spears *et al.* (1994 : 18S rDNA sequences, tree inferrence with PAUP and neighbor joining), with a result very similar to that seen in Fig. 1. An important difference is the position of the ascothoracidan (*Ulophysema oeresundense*, discussed below). The dendrogram is for the most part plausible, with few important exceptions : *Daphnia galeata* (Branchiopoda : Cladocera) is grouped with an ostracod and not with anostracans. *Diastylis sp.* does not appear close to the other malacostracans (Decapoda). Since these results are not acceptable for a taxonomist familiar with crustacean morphology, one must ask whether other clades could also be misleading.

A spectrum of group-supporting positions (Fig. 2) calculated as explained in the previous chapter, shows that only few of the groups of Fig. 1 are supported by a large number of sequence positions (Thoracica + Rhizocephala, Anostraca, Chelicerata, Acrothoracica, Thoracica). A clear ***limit of uncertainty*** which indicates how many positions are needed for a reliable hypothesis of monophyly does not exist. It could be calculated using a ***model of sequence evolution***, but it seems to be safer to use empirical observations : the unacceptable group *Daphnia* + *Stenocypris* is supported by 20 positions, which must be chance similarities (a "long branch problem"; this number is exceptionally high; combining other unrelated species this data set yields 0 to rarely more than 5 supporting positions). Many of the groups with even lower number of supporting positions are without doubt monophyletic (e.g. Cirripedia, Decapoda), but we must accept the fact that only little phylogenetic signal is conserved in 18SrDNA for these groups, wherefore a cladistic analysis will always be risky (see also Lanyon 1988). More information is needed.

It is particularly typical that of the early radiation of arthropods little signal is conserved. Many Crustacea are highly evolved; stem-lineage crustacean apomorphies have probably been substituted. The signal in favour of non-crustacean taxa (1 polychaet, 2 chelicerates) seen in Fig. 2 (outgroup of Crustacea) is an artefact caused by plesiomorphies present in these outgroup sequences while there is a lack of signal in ingroup (crustacean) sequences.

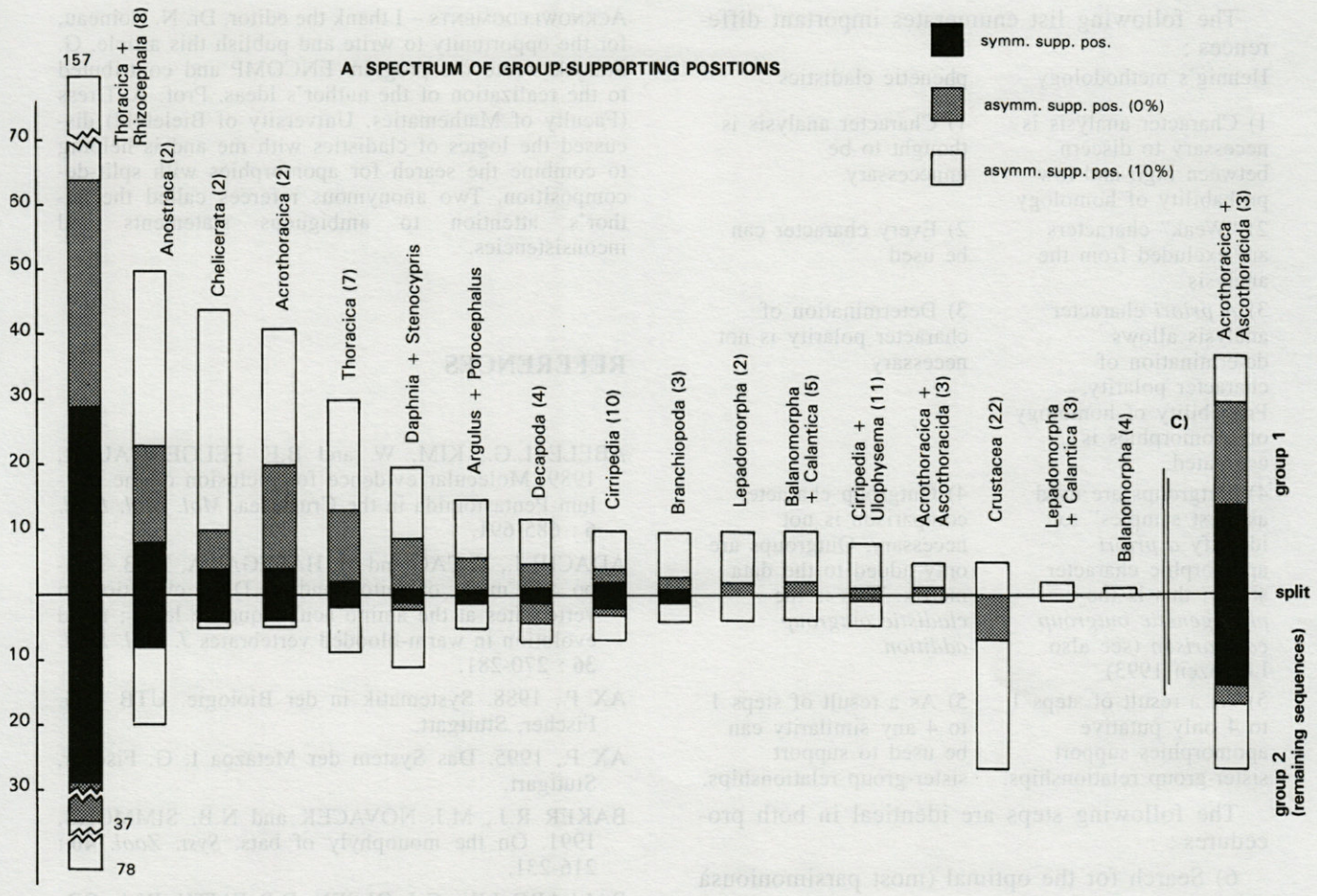
Effects of plesiomorphies can also be demonstrated for the artificial group Acrothoracica + Ascothoracida, which is seen in dendrograms but is not supported by secondary structure (Spears *et al.* 1994). A strong signal is obtained for this group when only thecostracan sequences are used with *Branchinecta packardi* as single outgroup (Fig. 2, detail C). The outgroup sequence is highly derived, plesiomorphies present in the ascothoracidan and acrothoracican sequences are absent in *Branchinecta packardi*, causing support of a group based on plesiomorphies. As soon as more outgroup sequences are used (Fig. 1, 2), this signal disappears.

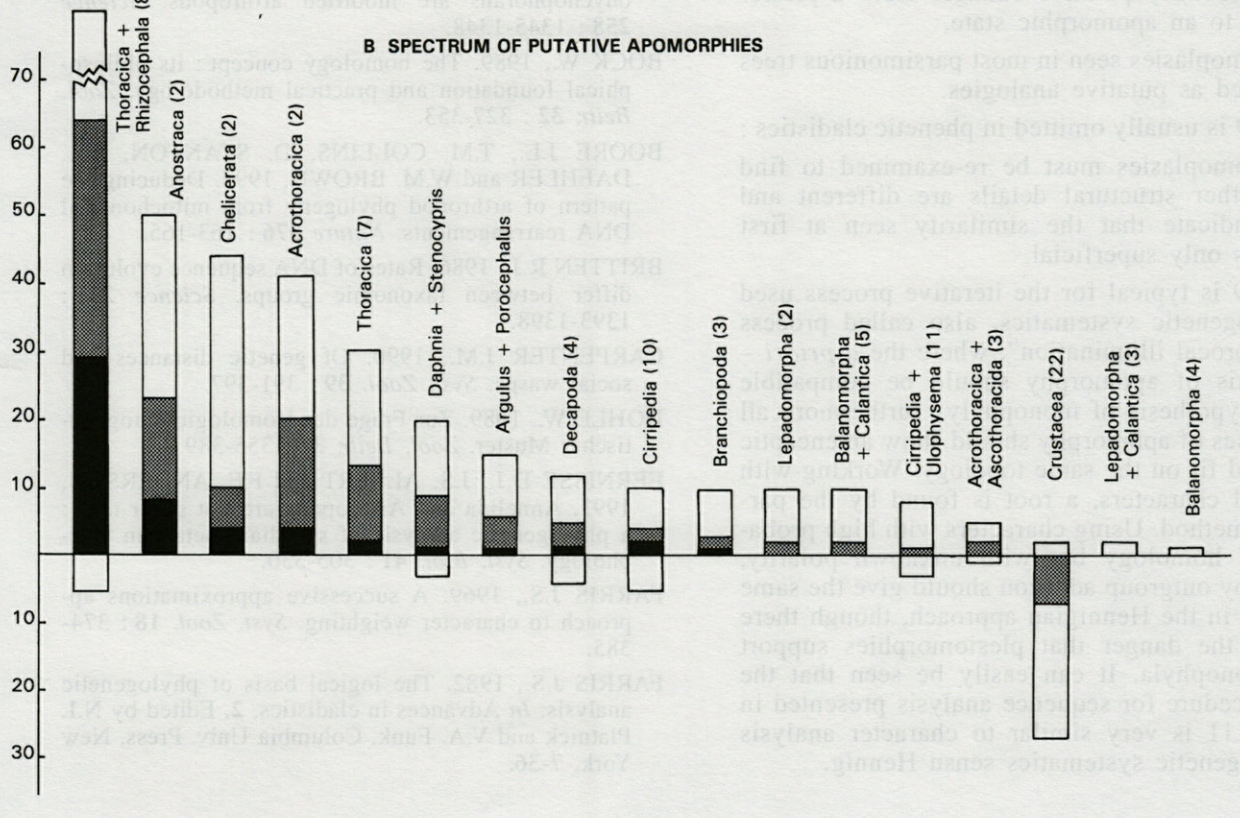
The number of putative apomorphies found in the spectra have been added to the tree in Fig. 1. Clades supported by a high number of putative apomorphies show a bootstrap value of 100%. Other high boostrap values are caused by character compatibility on the tree and not by high information content of the data. Future empirical observations of this kind must show how much sequence information is needed to identify groups that, with a high probability, are monophyletic.

13. ON THE METHODOLOGICAL DIFFERENCES BETWEEN PHYLOGENETIC SYSTEMATICS SENSU HENNIG AND PHENETIC CLADISTICS

Phenetic cladistics is defined here as phylogeny inference without consideration of character analysis (Chapter 10). This is not an attack against the principle of parsimony, quite the reverse is true : the principle of parsimony must also be applied to the first step of a phylogenetic analysis, namely for estimation of probability of homology (see Chapter 7) of putative apomorphies. An analysis is Hennigian not because the data are good, but because the first step of the analysis (search for informative putative apomorphies) is not missing : a crucial principle of Hennig's approach is grouping according to synapomorphy (e.g. Farris 1986).

Fig. 2. – Spectrum of group supporting positions A) and of putative apomorphies B) obtained for the sequences of fig. 1 as explained in Chapter 11). For detail C) (upper right) only sequences of thecostracans and of *Branchinecta packardi* were used (explanation in text). The horizontal line represents the split between groups, the vertical axis the number of sequence positions. *Symm. supp. pos.* : symmetrical supporting positions; *asymm. supp. pos. (0%)* : asymmetrical supporting positions with no deviations; *asymm. supp. pos. (10%)* : asymmetrical supporting positions with deviations in up to 10% of the sequences.


A SPECTRUM OF GROUP-SUPPORTING POSITIONS
symm. supp. pos.
asymm. supp. pos. (0%)
asymm. supp. pos. (10%)
157
37
78
70
60
50
40
30
20
10
10
20
30
Thoracica + Rhizocephala (8)
Anostraca (2)
Chelicerata (2)
Acrothoracica (2)
Thoracica (7)
Daphnia + Stenocypris
Argulus + Porocephalus
Decapoda (4)
Cirripedia (10)
Branchiopoda (3)
Lepadomorpha (2)
Balanomorpha + Calantica (5)
Cirripedia + Ulophysema (11)
Acrothoracica + Ascothoracida (3)
Crustacea (22)
Lepadomorpha + Calantica (3)
Balanomorpha (4)
Acrothoracica + Ascothoracida (3)
C)
split
group 1
group 2
(remaining sequences)


B SPECTRUM OF PUTATIVE APOMORPHIES
70
60
50
40
30
20
10
10
20
30
Thoracica + Rhizocephala (8)
Anostraca (2)
Chelicerata (2)
Acrothoracica (2)
Thoracica (7)
Daphnia + Stenocypris
Argulus + Porocephalus
Decapoda (4)
Cirripedia (10)
Branchiopoda (3)
Lepadomorpha (2)
Balanomorpha + Calantica (5)
Cirripedia + Ulophysema (11)
Acrothoracica + Ascothoracida (3)
Crustacea (22)
Lepadomorpha + Calantica (3)
Balanomorpha (4)
functional ingroup

The following list enumerates important differences :

Hennig's methodology	phenetic cladistics
1) Character analysis is necessary to discern between high and low probability of homology	1) Character analysis is thought to be unnecessary
2) "Weak" characters are excluded from the analysis	2) Every character can be used
3) *A priori* character analysis allows determination of character polarity. Probability of homology of apomorphies is estimated.	3) Determination of character polarity is not necessary
4) Outgroups are used as "test samples" to identify *a priori* apomorphic character states; this is the *phylogenetic outgroup comparison* (see also Lorenzen 1993)	4) Outgroup character comparison is not necessary. Outgroups are only added to the data matrix. This is the *cladistic outgroup addition.*
5) As a result of steps 1 to 4 only putative apomorphies support sister-group relationships.	5) As a result of steps 1 to 4 any similarity can be used to support sister-group relationships.

The following steps are identical in both procedures :

6) Search for the optimal (most parsimoniousà tree,

7) character state changes seen on a branch are used to identify putative changes from a plesiomorphic to an apomorphic state,

8) homoplasies seen in most parsimonious trees are valued as putative analogies.

Step 9 is usually omitted in phenetic cladistics :

9) Homoplasies must be re-examined to find out whether structural details are different and really indicate that the similarity seen at first glance is only superficial.

Step 9 is typical for the iterative process used in phylogenetic systematics, also called process of "reciprocal illumination", where the *a priori* – hypothesis of apomorphy should be compatible with a hypothesis of monophyly; furthermore all hypotheses of apomorphy should show an encaptic order and fit on the same topology. Working with polarized characters, a root is found by the parsimony method. Using characters with high probability of homology but with unknown polarity, rooting by outgroup addition should give the same result as in the Hennigian approach, though there remains the danger that plesiomorphies support false monophyla. It can easily be seen that the new procedure for sequence analysis presented in Chapter 11 is very similar to character analysis in phylogenetic systematics sensu Hennig.

ACKNOWLEDGMENTS – I thank the editor, Dr. N. Coineau, for the opportunity to write and publish this article. G. Stanjek wrote the program ENCOMP and contributed to the realization of the author's ideas. Prof. A. Dress (Faculty of Mathematics, University of Bielefeld) discussed the logics of cladistics with me and is helping to combine the search for apomorphies with split-decomposition. Two anonymous referees called the author's attention to ambiguous statements and inconsistencies.

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Reçu le 11 janvier 1996 ; received January 11, 1996
Accepté le 26 février 1996 ; accepted February 26, 1996

VIE MILIEU, 1996, 46 (2) : 139-153

OF UROPODS AND ISOPOD CRUSTACEAN TREES : A COMPARISON OF "GROUNDPATTERN" AND CLADISTIC METHODS

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CLADISTICS
COMPUTERISED METHODS
PHYLOGENETICS
CRUSTACEA
ISOPODA

ABSTRACT. – In a recent paper, Wägele (1994) attacked widely used computer-assisted cladistic methods for estimating phylogenetic trees, specifically those used in isopod phylogeny. This paper evaluates his alternative method, based on the allegedly "Hennigian" determination of groundpatterns, and compares it with empirical cladistic methods. Wägele's groundpattern method for determining phylogenies is logically circular, because it finds monophyletic groups that were assumed in the assembly of the groundpatterns. The method is also unscientific because it does not test the hypotheses that it proposes. Trees obtained using this method are likely to be unparsimonious because characters are not evaluated globally. As examples of how Wägele's method fails, and how cladistic methods are more rigorous, three cases from isopod phylogeny are discussed in some detail : the distribution of character states in the uropods, the sister groups of the Protognathiidae, and the relationships of taxa in the Microcerberidae.

CLADISTIQUE
MÉTHODES INFORMATIQUES
PHYLOGÉNIE
CRUSTACEA
ISOPODA

RÉSUMÉ. – Dans une publication datant de 1994, Wägele critique les méthodes cladistiques informatiques par la reconstruction des arbres phylogénétiques, et en particulier celles qui ont été utilisées pour la phylogénie des Isopodes. Cet article évalue une méthode alternative basée sur l'élaboration de "groundpatterns" méthode prétendue "hennigienne", puis la compare avec les méthodes cladistiques empiriques. La méthode du groundpattern de Wägele pour reconstruire les phylogénies est circulaire, car elle retrouve les groupes monophylétiques qui étaient déjà présumés dans l'ensemble des groundpatterns. Ce procédé est également peu convaincant car il ne teste pas l'hypothèse qu'il propose. Les arbres ainsi obtenus ne sont pas parcimonieux car les caractères ne sont pas évaluées globalement. Trois exemples de la phylogénie des Isopodes sont discutés en détail afin de montrer les faiblesses de la méthode de Wägele et comment les méthodes cladistiques sont plus rigoureuses : la distribution des états des caractères des uropodes, les groupes frères des Protognathiidae et les relations entre taxons chez les Microcerberidae.

INTRODUCTION

Phylogenetic research has seen stormy times in the last century, with various methods of inference holding the scientific community's attention, and then being replaced by more explicit and rigorous techniques. Computer assisted cladistic methods are now commonly used for inferring the branching structure of evolution, and in the absence of time machines, we may not have much better in the near future. Some European workers nevertheless prefer an allegedly "Hennigian" style of "argumentation," and belabour "well interred criticisms" of cladistic methods (Cannatella, 1991 : 377; see also Janvier, 1991). This rift between empirical cladists and neohennigians seems unlikely to go away for largely sociological reasons (Nelson, 1993), but this paper clarifies the methods of one neohennigian practitioner with respect to maximum parsimony cladistic methods.

Wägele (1989a) presented an explicit branching diagram of the phylogeny of major taxa in the Isopoda based on a detailed discussion of character states, but without global optimisation of the characters. Brusca and Wilson (1991) compared Wägele's tree with cladograms found using a well defined data matrix. Wägele's tree was found to be unparsimonious and therefore a less probable hypothesis of phylogeny. The most parsimonious

trees found by Brusca & Wilson (1991) also suggested different paths of character evolution and a different classification from those of Wägele (1989a). Recently, Wägele (1994; Wägele *et al.*, 1995) has dismissed the Brusca and Wilson (1991) cladograms for the isopod crustaceans as "simplistic" and "based on methodological error." Wägele's premise is that the cladogram (in his opinion) was wrong, so the method must be wrong. Because Wägele, in a series of papers (Wägele, 1994, 1995; Wägele *et al.*, 1995; Wägele and Stanjek, 1995), attacks analytical paradigms in modern phylogenetics, his initial 1994 paper is discussed in some detail here. In so doing, I clarify the differences between empirical cladistic methods that use global parsimony analysis and Wägele's (1989a; 1994) method of phylogenetic construction, which depends on what he calls "groundpatterns" (not to be confused with Wagner's (1980) groundplan divergence method). Wägele (1994) is in the same vein as an earlier critique of computer assisted cladistic methods (Lorenzen and Sieg, 1991), which was shown to be seriously flawed and invalid (Pleijel *et al.*, 1992; Meier and Whiting, 1992; Haszprunar, 1992). The inadequacies of Wägele's "groundpattern" method are explained below, with a few examples from isopod phylogeny. Wägele (1994) is not answered point by point, because several issues he raises will be dealt with in later papers. In the following, "Wägele" means the paper of Wägele (1994), and page citations are from that work.

GROUNDPATTERNS

The notion of groundpatterns is central to Wägele's (1989a; 1994; Wägele *et al.*, 1995; Wägele and Stanjek, 1995) method of constructing allegedly "Hennigian" phylogenies. A groundpattern of a taxon is an assemblage of presumed *ad hoc, a priori* ancestral character states. The groundpattern represents either a terminal taxon or an hypothetical ancestor within a phylogenetic tree. The construction of a groundpattern apparently relies on phylogenetic information external to the analysis at hand. That is to say, early in the analysis (e.g. Wägele's Fig. 1), polarities are determined for each character based on *a priori* knowledge of hypothetical relationships. The groundpattern is then constructed from these assumed plesiomorphic features of group of taxa. Wägele (p. 82) states that a groundpattern is "... reconstructed by analysis of the phylogeny of subordinated taxa after the reconstruction of the groundpatterns of these subordinated taxa." Groundpatterns, therefore, are "'basal node characters' or 'ancestral states'" that are "reconstructed in a previous analysis" (p. 85).

Wägele's groundpattern analysis differs from the determination of ancestral states often used in empirical cladistic analyses. Ancestral character states are generally constructed for entire ingroups or for terminal taxa using outgroup analysis (Maddison *et al.*, 1984) or using ontogenetic information (Nelson, 1978). Lundberg rooting (Lundberg, 1972; Swofford, 1990) is sometimes used in cases where suitable outgroups are unavailable to root an undirected tree (e.g. for the Onychophora: Reid, 1996). In Lundberg rooting, undirected trees obtained in a parsimony analysis are rooted using a hypothetical ancestor, defined only by those character states for which an *a priori* determination of polarity is possible. Many or most characters for a hypothetical ancestor in Lundberg rooting need not be defined. Wägele, on the other hand, believes groundpatterns should be constructed sequentially for all characters during each step of a phylogenetic analysis to build a tree.

The greatest weakness of groundpatterns is how one determines their membership. One must rely on arguments of monophyly to assemble the taxa of a groundpattern. A groundpattern thus assumes that which is being sought in a phylogenetic analysis; i.e., it provides data for a hypothesis of relationships, but is dependent on that hypothesis for its description. This method is also error prone because Wägele (1989a; 1994) seems to rely on previously published ideas for determining ground pattern membership. For example, his groundpattern grouping for a sister group of the Asellota includes the Calabozoidae, because van Lieshout (1983) in her original nonphylogenetic paper highlighted what she thought were asellotan features. The Protognathiidae is grouped with the Gnathiidae because Wägele assumes that the two groups are closely related using results from an earlier paper (Wägele and Brandt, 1988). Wägele (1989a, 1990; 1994) believes that the Microcerberidae are nested within the Asellota based on an earlier analysis (Wägele, 1983a), and therefore does not test the possibility that his or other classifications of this group may be incorrect (Brusca & Wilson, 1991). These issues are treated in the sections below.

Wägele (pp. 102-103) is concerned that computerised cladistics fails to recognise the "encaptic order" of the taxa, by which he means taxa nested within other taxa are used in a single analysis as separate entities. This "encaptic order" is an essential part of the groundpatterns, because some groundpatterns have other groundpatterns nested within them. Brusca & Wilson (1991) tested hypotheses of relationship by using both subordinate taxa and more inclusive taxa as separate entities in the same analysis, such as the Microcerberidae and the Asellota. In Wägele's (1983a, 1989a) classification, the Microcerberidae are a derived member of the Asellota. Wägele finds Brusca &

Wilson's (1991) use of the two taxa disturbing because it violates his groundpattern groupings. Nevertheless, if one decides that one taxon is nested within another and excludes the first taxon from the analysis (as Wägele does), one cannot test the validity of that nesting.

PHYLOGENETIC "ARGUMENTATION" USING GROUNDPATTERNS

The "Hennigian" analysis is "carried out 'descending' step by step, starting with small taxonomic units,..." (p. 84). Wägele (1994) and Sieg (oral communication, 1990 Crustacean Conference, Brisbane Australia) claim that all possible trees need not be considered because the characters determine the phylogeny. "It is a mistake to belief [*sic*] that relationships of a large number of taxa can be explored only with computer programs. The number of possible taxa [sic] combinations decreases rapidly with each correctly identified synapomorphy" (p. 104). The operative words in the last quote are "correctly identified synapomorphy." For Wägele, a synapomorphy becomes "correct" because he uses a preconceived notion of phylogeny. In this view, one simply builds the tree by adding larger and larger blocks of taxa, associated by the groundpattern characters (e.g., his Fig. 4). Therefore, that the number of hypothetically possible trees increases polynomially with the number of taxa (Felsenstein, 1978) is not an issue, because each synapomorphy limits the number of possible trees to a very small set. This method is similar to that used in the first, non-definitive step of a computerised analysis : finding a starting tree (= hypothesis) upon which to swap branches (e.g., the "closest" method in PAUP).

Wägele's groundpattern method runs afoul of homoplasy and parsimony – if you have independent characters that provide conflicting evidence of descent, how do you resolve a phylogeny? Global homoplasy is not a problem in Wägele's "descending reconstruction" method because the characters are not optimised across the entire tree but only among the groundpattern groupings previously determined. Therefore, a potentially homologous character state appearing in other presumptive clades/groundpatterns has no significance. Global parsimony is ignored; in fact parsimony itself is largely ignored. Such "argumentation" allows Wägele (1989a; 1994), for example, to assert that the uropod is repeatedly modified from the groundpattern state of the tailfan form (see below for further discussion). Wägele claims he is using parsimony in his method (e.g. the nearly unintelligible section on "evolutionary parsimony", p. 101), but his groundpattern grouping method denies global parsimony, i.e., across the entire tree, and makes no attempt to minimise homoplasy.

Wägele appears to confuse "synapomorphy" with "autapomorphy" (e.g., pp. 91, 93, 98; also in Wägele, 1995 : 45-46), but his misuse of the latter term may clarify the underlying method of groundpattern analysis. Ordinarily one uses the word "autapomorphy" for a unique derived character that is found only in one terminal taxon. An autapomorphy is therefore uninformative about cladistic relationships, although it may define a single terminal taxon. Wägele uses "autapomorphy" to refer to a derived character shared by several terminal taxa being analysed, where most systematists would use the term "synapomorphy", a shared derived character. Wägele is misusing the term, but in the context of his groundpattern analysis, however, "autapomorphy" refers to a hypothetical taxon with an apomorphic feature. This then is the essence of groundpattern analysis : synapomorphies are converted into autapomorphies by coalescence of terminal taxa into a single groundpattern; the terminal taxa are thus removed from consideration. During the groundpattern tree reconstruction method, the analytical universe (set of analysed taxa) is reduced at each node deeper into the tree. Wägele's use of terms indicates this is being done during the analysis. The method fails at this point because falsifiability and parsimony are denied. By sequentially reducing the effective tip taxon number during a groundpattern analysis, Wägele's method increasingly removes parts of the tree from testing with the parsimony criterion. Consequently, a phylogeny estimated by this method is not scientific in the Popperian sense. Parsimony is simply ignored – no attempt at global minimisation of character state transitions is made. In contrast, empirical cladistic methods do not change the analytical universe during analysis; a cladogram derived by these methods, therefore, is a simultaneously parsimonious hypothesis of relationships for all taxa included.

Wägele's attack (p. 85) on the concept of the OTU (operational taxonomic unit) comes from the same source as his inability to tell a synapomorphy from an autapomorphy. Wägele asserts that OTU "smokescreens the indispensable reconstruction of groundpatterns." He dislikes this concept because an OTU presumes that all taxa will be used in the construction of a tree, while he thinks that only his groundpatterns should be used to construct the tree. By sequentially reducing the set of taxa or groundpatterns during tree building, he simplifies his analysis but, as pointed out above, fails to achieve a global solution.

The appearance of different, more parsimonious topologies in Brusca & Wilson (1991) is therefore not surprising. Wägele's groundpattern method is

logically circular. Although he accuses Brusca & Wilson (1991) of this error, no such error was committed (see below). Circular logic is simply where the data used to choose a hypothesis depend on the same hypothesis for their existence. In a phylogenetic analysis using groundpatterns, this occurs when a hypothesis of relationship is used to determine the data that are then used to choose the same hypothesis. Wägele (1989a; 1994; Wägele *et al.*, 1995; Wägele and Stanjek, 1995; Wägele, 1995), therefore, sequentially assembles presumed monophyletic groups, determines their groundpattern states and finishes with a global hypothesis that contains the previously determined groups. No scientific test occurs in Wägele's groundpattern method : he simply piles taxa together in an *ad hoc* fashion.

CLADISTICS AND PARSIMONY ANALYSIS

How cladistic computer programs work

In the "subjectivity of computer cladistics" (p. 84), Wägele criticises 'computer cladistics,' but lists things inherent in any phylogenetic method. Wägele also claims that cladistic computer programs "calculate the tree." In this, he appears to misunderstand how a maximum parsimony analysis simultaneously and globally uses the information in all characters. In empirical cladistic methods, trees are chosen on the basis of their ability to parsimoniously explain the distribution of character states among all taxa with the fewest possible *ad hoc* hypotheses of character change. Using parsimony analysis, a universe of all possible solutions is systematically narrowed down to the fewest equally most probable solutions. Therefore, trees are not calculated, but are tested with the data using the parsimony criterion. Modern cladistic methods are most assuredly not "phenotypic" (p. 97) [*sic* – "phenetic" may be the meant]. Wägele thus confounds phylogenies and phylogenetically informative data, and may not be aware of the epistemological implications of his own groundpattern analysis.

Using the criterion of maximum parsimony, a cladogram (representing the branching order of a phylogeny) is chosen by observing how characters change on its branches. Although fully elucidated in several sources (e.g. Wiley, 1981; Swofford, 1990; Swofford & Olsen, 1990; Forey *et al.*, 1992), the following simplified explanation is provided for comparison with Wägele's method. First, the character changes are plotted on a tree so that the number of changes or transitions are minimised. Next, the changes are summed for all characters on all branches, providing the total number of transitions for the tree, the "tree length." The first tree in an analysis is retained for comparison with other trees. How the first tree is obtained is unimportant, except for optimising the time needed to find the shortest trees. Then another tree is obtained by some method (variations of branch re-arrangements), and the number of character changes summed as before. The new tree length is compared with the previous sum of character transitions, and the shortest tree of the two is retained. This process is continued until all shortest trees are found. During this tree comparison process, the characters are not used to calculate the tree, as Wägele (also quoted from Neff, 1986) implies, but the characters are used to choose a tree topology. The tree topology is constructed independently of the characters. But because the distribution of character states reflects the evolutionary process, the tree that is most congruent with the characters will be the best estimate of the phylogeny.

In parsimony methods, the simplest hypothesis is chosen as the most probable. The Popperian point of view asserts that the most probable complex hypothesis is that which is rejected the fewest times, thus suggesting a criterion for minimisation. For computer assisted cladistic applications, the appropriate criterion to be minimised is tree length, the sum of all hypothetical character changes (i.e, evolutionary transitions). For the method to work, the trees must be chosen independently of the character data, or the method becomes circular or at least starting point dependent (i.e., different starting points yield different results). For this reason, I prefer random starting tree topologies (available in the computer programs PAUP – Swofford, 1990 and PHYLIP – Felsenstein, 1993), because no assumptions are made about the distribution of character states during the initial tree construction. A tree must succeed over other possible trees based only on its parsimonious explanation of the data. Computer programs figure in this process because many tree topologies must be tested, and topologies with even small numbers of taxa may have millions of possible trees (Felsenstein, 1978). Wägele (p. 81) believes that computer programs are used as "black boxes" but anyone who uses a particular program should understand what the program is doing, or the interpretation of the results becomes equivocal. Most cladists do not have a "blind belief" in computer programs and, in fact, are constantly alert for programming algorithms that may violate the underlying cladistic logic (e.g. Luckow & Pimentel, 1985; Platnick, 1989; Coddington and Scharff, 1995). Much effort has been devoted to evaluating the accuracy of computerised phylogenetic methods (Hillis, 1995; Huelsenbeck, 1995; Li and Zharkikh, 1995; Miyamoto and Fitch, 1995). Although cladistic computer programs do not provide Wägele's "hand calculated"

results, one should not suspect the programs are wrong (Pleijel *et al,* 1992; Meier and Whiting, 1992). Wägele's groundpattern method may be the problem. His method cannot be heuristically useful because it determines tree structure from a priori hypotheses of relationship, and does not make independent comparisons of alternative trees. Computers may indeed be "black boxes" for Wägele because he appears to confuse maximum parsimony analysis with a distance analysis : Wägele (1995 : 45, his Fig. 3) discusses a distance tree in a parsimony context.

Necessity of polarising the characters

Despite Wägele's strident claims to the contrary, characters do not need to be polarised prior to a maximum parsimony cladistic analysis (Clark and Curran, 1986), except in Lundberg rooting or in some other parsimony methods that require some (but not all) characters to be polarised (e.g. Dollo or Camin/Sokal methods : Farris, 1977; Camin & Sokal, 1965). The character states must be homologous, but *a priori* choice of the direction and the pattern of changes is not necessary to find a parsimonious tree. In many cases, this is a strength of computer assisted cladistic analysis, because the *a priori* assignment of polarity to character transitions requires *ad hoc* arguments. While some character states may be objectively classified as apomorphic, in many cases one cannot be certain that an assessment of polarity and/or direction is correct, as happens for many characters of the Isopoda. Outgroup rooted maximum parsimony analyses are needed to achieve an unbiased assessment of the polarity of the characters simultaneously with that of the tree topology. The congruence of all characters on a parsimonious topology is an objective criterion for assigning apomorphies.

Use of outgroup taxa

In "Character valuation – an *a priori* source of mistakes", Wägele (p. 85-86) writes that using outgroups to provide "character polarity" is a "logical mistake : only the groundpattern of the ingroup contains the plesiomorphies that could be used for this procedure..." Wägele is apparently unaware of the implications of his statement. The groundpattern is a hypothetical construct that is obtained prior to the estimation of a phylogeny. The groundpattern does not contain anything because it does not exist – it is only a hypothesis similar to an *ad hoc* hypothetical ancestor, but with the difference that the latter does not require the monophyly of the ingroup to be certain. We cannot determine a groundpattern from inspecting an animal and we cannot be certain that the groundpattern has anything to do with the ancestral states of a taxon. A phylogenetic estimate based on a predetermined hypothesis of descent must be circular in construction, and is one weakness of Wägele's method.

Wägele also claims (p. 84) that the use of outgroup taxa in an analysis is a subjective procedure, despite widespread opinion to the contrary (Maddison *et al.*, 1984; Kitching, 1992; Nixon and Carpenter, 1994). His belief is based on the assumption that one must be certain of the monophyly of the ingroup and the sister groups of the ingroup, using an a priori analysis. This assumption is incorrect. The use of outgroups in an analysis can test the monophyly of the ingroup, as was done in Wilson (1994) for the isopod family Janiridae. A more robust, objective analysis of relationships results from the inclusion of several outgroups (Maddison *et al.*, 1984), and decreases the chance that an inappropriate taxon will distort the rooting. Multiple outgroups provide the best ancestral optimisation at the outgroup node. Wägele also asserts that (p. 90) "Prior to the cladistic analysis, character analysis requires outgroup comparisons and – for terminal taxa – the reconstruction of ground patterns." Only in Wägele's idiosyncratic method (see also Wägele, 1995) is this necessary.

Character states of Terminal taxa

On p. 91 Wägele states : "To use computer programs, prior to the assemblage of a data matrix, groundpatterns must be reconstructed for all terminal taxa, whenever these are not species. To avoid mistakes, only groundpattern characters can be used for the data matrix." Groundpatterns are not necessary for phylogenetic analysis, and should be avoided because of the subjective element they introduce. The character states in a matrix are determined from the diagnoses of the terminal taxa. These are observed features, not idealised character states where the evolutionary direction has been interpreted, perhaps wrongly. If characters vary in the terminal taxa, as often happens, one has several options depending on the goals of an analysis.

1. Add terminal taxa to the tree to account for all variants (e.g. Struwe *et al.*, 1994). This is probably best alternative because it tests the monophyly of the terminal taxon. This method becomes computationally difficult when the number of variants is high in terminal taxa. Care must be taken to avoid combinations that do not occur in nature.

2. Use the multistate taxon option (as implemented in PAUP). This option allows the terminal taxa to have several character states during an

analysis, and can be used when polymorphism is observed in a species level taxon. This option may be used for higher level taxa, although one should demonstrate that the terminal taxon is monophyletic. This method is generalised by scoring the character as "unknown," allowing any state to be considered for a multistate taxon.

3. Use only the state found in the type species of the terminal taxon. This will guarantee precise results for a particular classification. This method does not test for nonmonophyly of a terminal taxon. Aberrant type species may also decrease the generality of such analyses.

4. Use the plesiomorphic state within the taxon, as was done in Brusca & Wilson (1991). This last option is closest to Wägele's "groundpattern" character analysis, but it is only used for terminal taxa and only for the characters where several states were observed in a terminal taxon. Wägele extends this method throughout the tree during tree construction, a procedure even less compatible with objective phylogenetic estimation. Maximum parsimony analysis makes no such attempts.

Tests of Cladograms

In his "Circular tree comparison" section (p. 103), Wägele appears to misunderstand phylogenetic arguments and even the nature of a circular argument. His Figure 11 shows a comparison of "dendrograms" from two different data sets, and asserts that this is circular argumentation, another "mistake" he finds in Brusca & Wilson (1991). Despite these assertions, independent data sets are valuable for comparison of phylogenies. The best test of a cladogram (a more accurate term than "dendrogram") is to use a new and different data set (Miyamoto and Fitch, 1995). If a tree represents a robust phylogenetic hypothesis, it will be corroborated by the new data. This is not circular argumentation, as Wägele complains, but is an independent test of the cladogram because the data are independent of the cladistic hypothesis. The groundpattern method, on the other hand, is inherently circular because the data are not independent of the tree : the investigator develops a groundpattern of characters based on a priori notions of the phylogeny; the groundpattern is then used to build the phylogeny.

PHYLOGENETIC HYPOTHESES IN THE ISOPODA

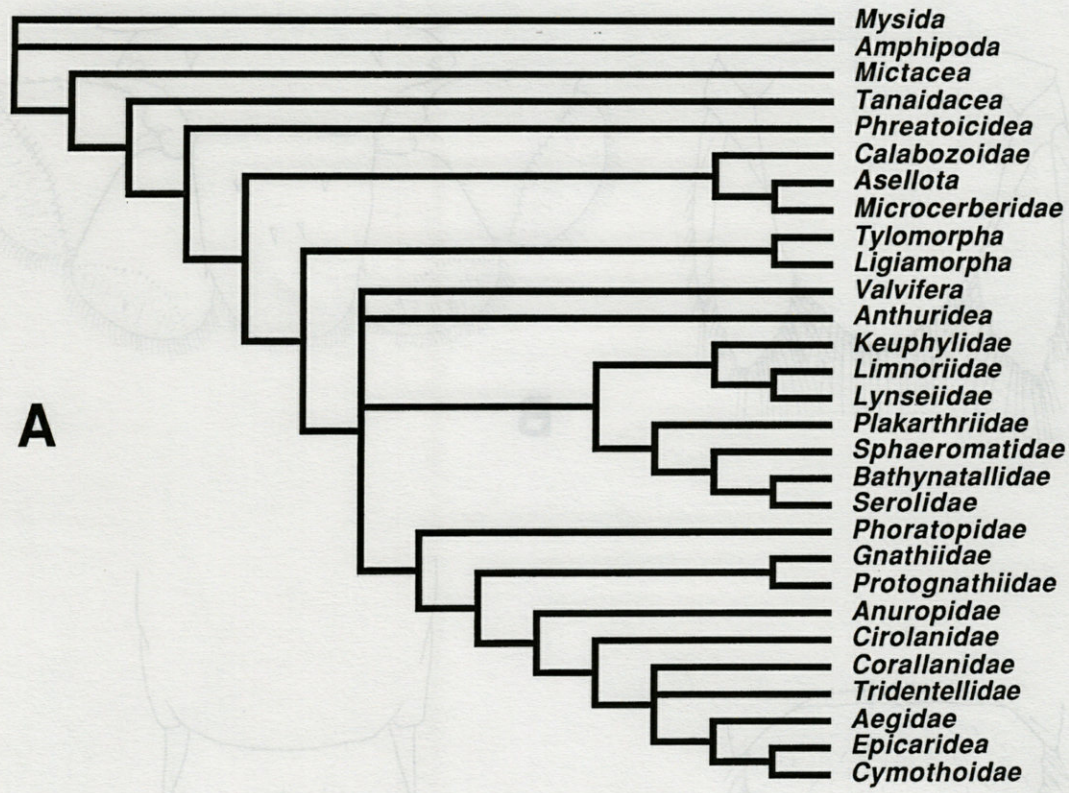
The strength of empirical cladistic methods is that trees are analysed without preconceived notions about descent, using the characters to test and either reject or accept particular phylogenetic hypotheses. The character state data contain the phylogenetic information that one wishes to recover. Under a criterion of maximum parsimony, the data used by Brusca & Wilson (1991) rejected the hypothesis of Wägele (1989a), and provided support for a different topology (Fig. 1). Although all of Wägele's points are not addressed here, a few important examples are selected.

Uropods

Wägele highlights the optimisation of uropod character states as a major difference between his phylogeny (Wägele, 1989a) and that of Brusca & Wilson (1991). Two generalised states of this character can be identified. "Tail fan" uropods (figs. 2A-B) have broad, flat rami and short protopods (basal article), while styliform uropods (Fig. 2C-D) have elongate protopods and rami. In Wägele's opinion, the tail-fan uropod of isopods (Fig. 2A) is similar to those of the Eucarida (Fig. 2B), so this state must be the isopod "groundpattern." The styliform uropods seen in all basally derived isopods (Fig. 2D) and in all possible outgroups are only multiple convergences, reductions of the basic tail fan. Therefore, he concludes that the Brusca & Wilson (1991) phylogeny must be in error. Wägele's (1989a,b; 1990; 1992a,b) theories regarding phylogeny, ecological adaptation and biogeography depend heavily on this idiosyncratic concept of uropod evolution. Nevertheless, the optimisation of the uropod states on either Wägele (1989a) or Brusca & Wilson (1991) trees (Fig. 1) results in an ancestral form that is unlike the Wägele isopod groundpattern uropod (Fig. 3).

Brusca & Wilson (1991) used multiple peracaridan outgroups to root the isopod cladogram, providing an objective status for the character states of the isopod outgroup node (Fig. 3). Most peracarid outgroups (Amphipoda, Cumacea, Mictacea, Tanaidacea) have styliform uropods. The taxa that emerge closest to the isopod part of the tree (Mictacea, Tanaidacea) have styliform (or non-tailfan) shaped uropods. The isopod taxa that branch off earliest in both versions of the phylogeny (Fig. 3) also have styliform uropods (e.g. *Crenoicus*, Fig. 2D). Parsimony demands that the simplest explanation, a styliform uropod, stands at the basal node (or "groundpattern") of the isopods.

Wägele, on the other hand, homologises the uropod of the Cirolanidae and other "flabelliferans" with basally derived malacostracans. Previous authors (Schultz, 1969; Hessler, 1969 : R372-373; Kensley and Schotte, 1989) have indicated that the Cirolanidae (Fig. 2A) and other flabelliferan families have the archetypical form of the Isopoda, primarily based on the fan-like



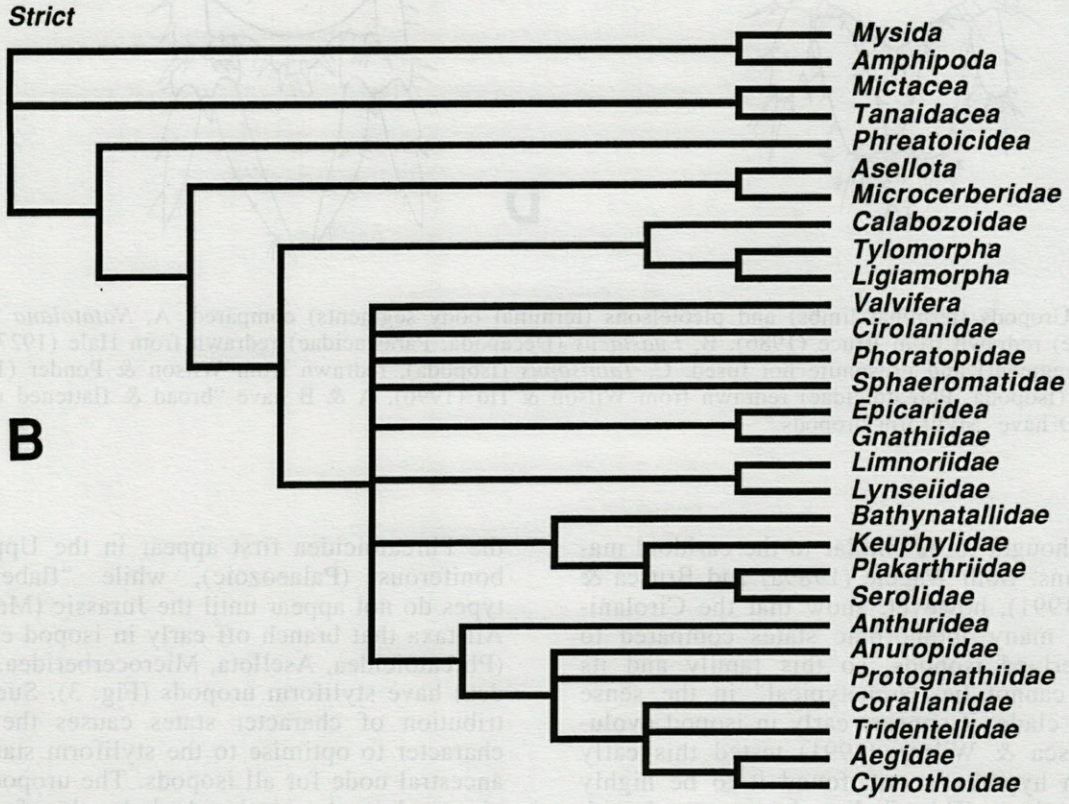


Fig. 1. – Two competing tree topologies for the Isopoda, with 4 peracaridan outgroups (Mysida, Amphipoda, Mictacea, Tanaidacea). A, topology of Wägele (1989a), as analysed by Brusca & Wilson (1991), tree length = 153. B, strict consensus tree from Brusca & Wilson (1991) of 16 equally parsimonious trees, tree lengths = 129. Trees drawn using PAUP (Swofford, 1990).

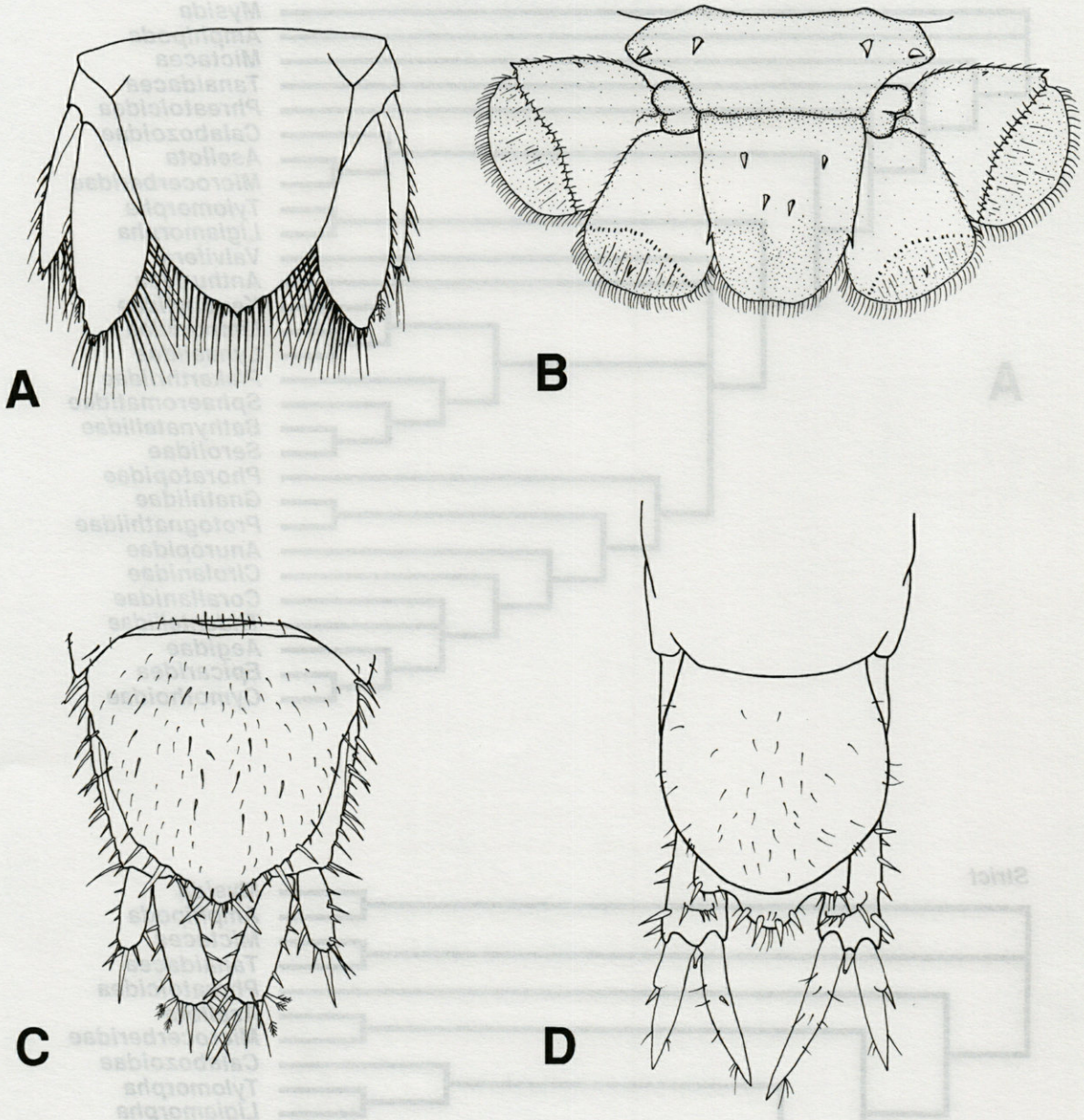


Fig. 2. – Uropods (terminal limbs) and pleotelsons (terminal body segments) compared. A, *Natatolana* (Isopoda, Cirolanidae) redrawn from Bruce (1986). B, *Euastacus* (Decapoda, Parastacidae) redrawn from Hale (1927); telson (terminal segment) and urosomite not fused. C, *Tainisopus* (Isopoda), redrawn from Wilson & Ponder (1992). D, *Crenoicus* (Isopoda, Phreatoicidae) redrawn from Wilson & Ho (1996). A & B have "broad & flattened uropods," and C & D have "styliform uropods."

uropods thought to be similar to the caridoid malacostracans. Both Wägele (1989a) and Brusca & Wilson (1991), however, show that the Cirolanidae have many apomorphic states compared to earlier derived isopods, so this family and its relatives cannot be "archetypical" in the sense that, as a clade, it appears early in isopod evolution. Brusca & Wilson (1991) tested this early derivation hypothesis and found it to be highly unparsimonious. This finding is in accord with the fossil record (Hessler, 1969; Schram, 1974): the Phreatoicidea first appear in the Upper Carboniferous (Palaeozoic), while "flabelliferan" types do not appear until the Jurassic (Mesozoic). All taxa that branch off early in isopod evolution (Phreatoicidea, Asellota, Microcerberidea, Oniscidea) have styliform uropods (Fig. 3). Such a distribution of character states causes the uropod character to optimise to the styliform state at the ancestral node for all isopods. The uropodal state observed in the cirolanid clade, therefore, must be a reversion to a fan-like state (Fig. 3).

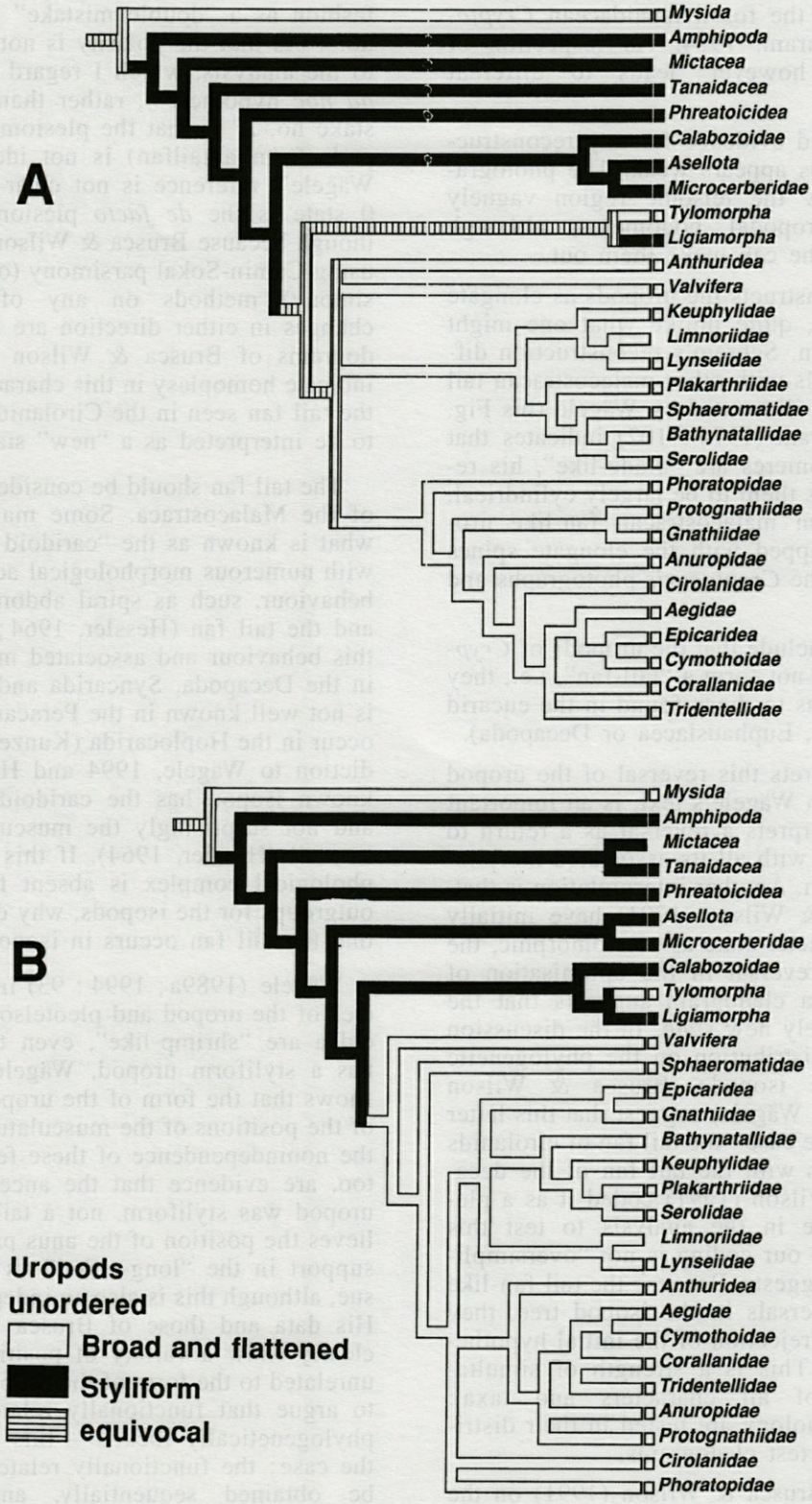


Fig. 3. – Distribution of uropod character states on two competing tree topologies for the Isopoda, with 4 peracaridan outgroups (Mysida, Amphipoda, Mictacea, Tanaidacea). Taxon names (state of terminal taxa) lacking small adjacent block indicates undefined or inapplicable states. A, topology of Wägele (1989a), as analysed by Brusca & Wilson (1991). B, One of 16 equally parsimonious trees of Brusca & Wilson (1991). Trees drawn using MacClade (Maddison & Maddison, 1992).

Wägele (1989a, 1994) believes that an uropodal tail fan occurs in the fossil tanaidacean *Cryptocaris hootchi* Schram, 1974. An inspection of Schram (1974), however, leads to different conclusions.

1. The published evidence for any reconstruction of the uropods appears weak. The photographed fossils show the telsonic region vaguely preserved the uropodal podomeres, although Schram indicates he can make them out.

2. Schram reconstructs the uropods as elongate with distal spines, quite unlike what one might regard as a tail fan. Schram's reconstruction differs in many details with other malacostracan tail fans such as those illustrated by Wägele (his Fig. 5). Although Schram (1974 : 102) indicates that the uropodal podomeres are "blade-like", his reconstruction shows them to be largely cylindrical. Moreover, caridean malacostracan fan-like uropods are not equipped with the elongate spines clearly shown in the *Cryptocaris* photographs and reconstruction.

Therefore, I conclude that the uropods of *Cryptocaris hootchi* do not form a "tail-fan", i.e., they are not homologous to those found in the eucarid Malacostraca (e.g., Euphausiacea or Decapoda).

How one interprets this reversal of the uropod form, alluded to in Wägele's text, is an important issue. Wägele interprets a reversal as a return to an ancestral state, with all its associated morphologies – an atavism. Another interpretation is that, although Brusca & Wilson (1991) have initially interpreted a character state as plesiomorphic, the appearance of a reversal in the optimisation of the character on a cladogram suggests that the feature is an entirely new state. In the discussion of the character distribution on the phylogenetic estimates for the isopods, Brusca & Wilson (1991 : ignored by Wägele) suggest that this latter interpretation is the case : the tail fan of cirolanids is not homologous with the tail fan of the decapods. Brusca & Wilson (1991) coded it as a plesiomorphic feature in the analysis to test this hypothesis, and so our coding is not "oversimplistic" as Wägele suggests. Because the tail fan-like uropod shows reversals in the isopod tree, they regarded this as a rejection of the initial hypothesis of homology. This is a strength of simultaneous analysis of all characters and taxa : hypotheses of homology are tested in their distribution on the shortest cladograms.

After quoting Brusca & Wilson (1991) on the standard method of evaluating characters as unordered, Wägele then asserts that "the analysis is numerical, and not phylogenetic" (p. 86). In this statement, Wägele demonstrates that he does not understand maximum parsimony and its function in phylogenetic analysis, nor does he accept the notion of homoplasy. He criticises our coding of uropods (0 = tail fan, 1 = styliform) in a simplistic fashion as a "double mistake" (p. 86). "Mistake no. 1" is that the polarity is not determined prior to the analysis, which I regard as a strength (no *ad hoc* hypotheses), rather than a mistake. "Mistake no. 2" is that the plesiomorphic state (uropods form a tailfan) is not identified correctly. Wägele's reference is not clear here because the 0 state is the *de facto* plesiomorphic state, although because Brusca & Wilson (1991) were not using Camin-Sokal parsimony (or irreversible parsimony) methods on any of the characters, changes in either direction are allowed. The cladograms of Brusca & Wilson (1991) therefore, indicate homoplasy in this character, which allows the tail fan seen in the Cirolanidae and other taxa to be interpreted as a "new" state, *a posteriori.*

The tail fan should be considered in the context of the Malacostraca. Some malacostracans have what is known as the "caridoid escape reaction," with numerous morphological adaptations for this behaviour, such as spiral abdominal musculature and the tail fan (Hessler, 1964; 1983). Although this behaviour and associated morphology occurs in the Decapoda, Syncarida and Euphausiacea, it is not well known in the Peracarida, and does not occur in the Hoplocarida (Kunze, 1981; in contradiction to Wägele, 1994 and Hessler, 1964). No known isopod has the caridoid escape reaction, and not surprisingly the musculature shows this as well (Hessler, 1964). If this behavioural/morphological complex is absent from all potential outgroups for the isopods, why does Wägele insist that the tail fan occurs in isopod groundpattern?

Wägele (1989a; 1994 : 93) indicates that muscles of the uropod and pleotelson in the Phreatoicidea are "shrimp-like", even though this taxon has a styliform uropod. Wägele's own evidence shows that the form of the uropod is independent of the positions of the musculature. If one accepts the nonindependence of these features, then they, too, are evidence that the ancestral form of the uropod was styliform, not a tail fan. Wägele believes the position of the anus provides additional support in the "long-tailed" vs "short-tailed" issue, although this is also an independent character. His data and those of Brusca & Wilson (1991) clearly show a variety of positions for the anus, unrelated to the form of the uropod. Wägele seems to argue that functionally related characters are phylogenetically locked – this proves to be not the case; the functionally related characters may be obtained sequentially, and largely independently. Attainment of a particular functional arrangement is a step-like process, with characters evolving separately. *Tainisopus* Wilson and Ponder, 1992 is a good example (Fig. 2C). This unusual isopod genus contains elongate, relatively unmodified isopods that have a broad pleotelson. Their uropods have the basal form, flattened sty-

liform, not the broad tail fan seen in the Cirolanidae. *Tainisopus* is a good swimmer (Wilson and Ponder, 1992), and yet does not have a tail fan.

Parsimony requires that the ancestral state for the Isopoda be a styliform uropod, i.e., not a tail fan. Wägele (1989a; 1994; see also Brusca & Wilson, 1991) indicates that the uropods are modified for many purposes and have many different morphologies within the isopods, so Wägele's evolution of the uropods becomes a weakly corroborated theory. Although one may decide that a feature must be plesiomorphic based on the distribution of states in some larger group of taxa, one may find that the concerted effect of many characters forces the feature to be a reversal. To deny the reversal is to deny parsimony.

How one interprets this rejection of homology is a matter for careful investigation of the characters involved. Wägele has done this but fails to parsimoniously interpret the data before him. He clings to his pet theory of the primacy of the tail fan homology, regardless of how much it is changed throughout the evolution of the peracarids. This tenacity may be based in his theoretical edifice based on an indefensible "just-so" story about ecological adaptations of the crustaceans to the evolution of fishes (Wägele, 1989b; 1992b). This case shows clearly that finding phylogenies using "groundpatterns" allows an investigator's preconceived ideas about evolution to colour the analysis.

Protognathiidae

An effective test of the trees of Wägele (1989a) and Brusca & Wilson (1991) comes from new information on the status of the genus *Protognathia* Wägele and Brandt, 1988. This taxon was originally proposed by Wägele and Brandt (1988) to be a "missing link" between the families Gnathiidae and Cirolanidae. The phylogeny of Wägele (1989a), not surprisingly, finds it to be a sister group of the Gnathiidae. Brusca & Wilson (1991) examined the descriptions of *Protognathia bathypelagica* (Schultz, 1977) and concluded that the Wägele and Brandt (1988) were in error about the maturity of the specimens. Other supposed synapomorphies of the protognathiid-gnathiid clade were shown by Brusca & Wilson (1991) to be not exclusively apomorphic. The strict consensus tree of Brusca & Wilson (1991) shows the Protognathiidae nested within a cirolanid clade as part of a three way polytomy that includes the Anuropidae and a corallanid-cymothoid clade (Fig. 1B, 3B). Gnathiidea is the sister group of the Epicaridea in a clade that is several branches removed from the Protognathiidae (Brusca & Wilson, 1991). This general topology is retained in recent cladograms resulting from analyses performed including *Tainisopus* Wilson & Ponder 1992 (Wilson, in prep.).

Recently, new data on *Protognathia* corroborates Brusca & Wilson's (1991) conclusion that the original specimens were immature, a point ignored by Wägele. A new specimen clearly assignable to *Protognathia* has been reported from the Antarctic (Kussakin and Rybakov, 1995) : an adult male with the full complement of seven pereopods, not six as in the Gnathiidae. The primary synapomorphy between Protognathia and Gnathiidea proposed by Wägele and Brandt (1988) and Wägele (1989a), lack of the last pair of legs in an adult, proves to be homoplasy caused by a "mistake" in their groundpatterns. These new data corroborate Brusca & Wilson's (1991) tree, and rejects the classification and phylogeny proposed by Wägele (1989a).

Microcerberidae

In the "Failure to recognise the encaptic order" section, Wägele (p. 102) criticises Brusca & Wilson (1991) on their use of a terminal taxon (Microcerberidae) in the analysis that is nested within another (Asellota). Wägele ignored our justification for doing so. The status of the Microcerberidae is being treated separately (Wilson, in prep.), but Brusca & Wilson (1991) clearly state that the Microcerberidae do not have the defining synapomorphies of the Asellota, one of which is the geniculate copulatory appendage on male pleopod II. Therefore, the Microcerberidae were included separately – thus conflicting with Wägele's (1983a) unparsimonious (Wilson, 1987) phylogeny of the Asellota. Brusca & Wilson's (1991) results were not intended to "prove" the specific classification of the two taxa, as Wägele (p.103) asserts. Because the status of the Microcerberidae has been a much discussed issue within isopod phylogenetics, it was informative for Brusca & Wilson (1991) to include this taxon in their analysis, where it appeared as the sister group of the Asellota.

Wägele *et al.* (1995 : their Fig. 7) present a "Scheme showing conspicuous steps in the evolution of the Microcerberidae" (see Fig. 4A) based on their Table 1 : "Salient characters of species of the Microcerberidae." An inspection of this table shows that most of the characters are autapomorphies and therefore uninformative phylogenetically. Analysis of these data with Hennig86 (Farris, 1988) or PAUP ver. 3 (Swofford, 1990) results, not surprisingly, in 9 shorter trees (e.g Fig. 4B), an unresolved strict consensus tree (Fig. 4C), a majority of which are not congruent (Fig. 4D) with the preferred topology of Wägele *et al* (1995). Moreover, one can easily dispute the polarisations of the characters in their Table 1.

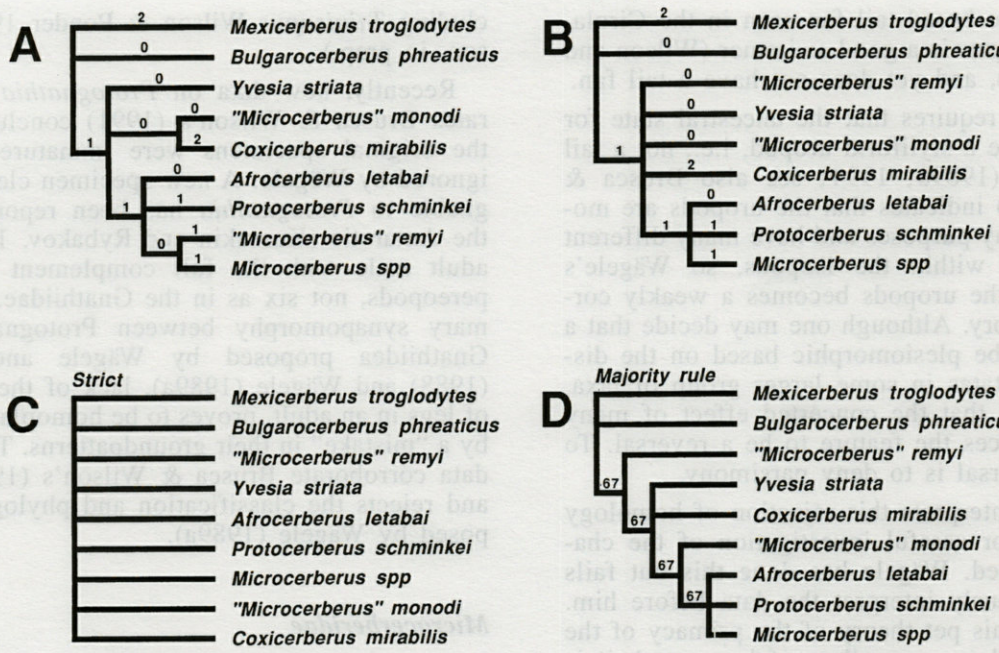


Fig. 4. Competing undirected cladograms for the Microcerberidae (Isopoda). A, topology from Wägele *et al.* (1995), tree length = 9 (or 3, uninformative characters excluded), with branch lengths (number of character state changes on a branch). B-D, topologies from 9 equally parsimonious trees found using the data of Wägele *et al.* (1995). B, one of 9 trees, length = 8 (or 2, uninformative characters excluded), with branch lengths. C, strict consensus tree. D, majority rule consensus tree, with branch percentages. Trees drawn using PAUP (Swofford, 1990).

For example, character 4 – the length of the fourth pleopod – depends on Wägele's assumption that microcerberids are asellotes : the plesiomorphic state would be short and covered by the previous pleopod, not long and protruding. By polarising the fourth pleopod character in a way that assumes asellotan ancestry, Wägele exposes the failure of his groundpattern method : it is unwilling to consider alternative hypotheses. Simply leaving the polarisation undecided, because either state could be plesiomorphic, is more objective.

Epistemological deficiencies in Wägele's groundpattern method lead to insupportable biogeographic schemes (Wägele's step no. 7, p. 83, in his "necessary steps in a phylogenetic analysis"). Wägele *et al.* (1995; also Wägele, 1983b, 1990) observe that the supposedly primitive species of Microcerberidae are found in fresh water, and that the derived species are marine. Wägele then jumps to the astonishing conclusion that microcerberids evolved in fresh water and then invaded the sea. His groundpattern method does not allow him to consider appropriate alternatives. Given that Wägele believes that microcerberids are asellotes, and that they are derived from asellotan taxa found only in fresh water (Wägele, 1983a), he concludes that the Microcerberidae plesiomorphically must be a fresh water group (Wägele, 1983b, Wägele *et al.*, 1995). A simpler alternative (abundantly demonstrated by the distribution of the Phreatoicidea : Birstein, 1962; Schram, 1974; Banarescu, 1990; Williams, 1980) is that the Microcerberidae evolved in marine waters and colonised fresh water. This transition to fresh water occurred in taxa that retain some plesiomorphic features, such as the exopod on the uropod. The marine microcerberids continued to evolve, and the ancestors of the freshwater taxa became extinct in the ocean, or are not yet discovered there. Evidence for this scenario may be derived from the observation that the sister taxon of the Microcerberidae, the Atlantasellidae (see phylogeny in Wägele, 1983a; corroborated by unpublished data), is marine. If the outgroup is marine and the ingroup contains both marine and fresh water taxa, it is simplest to interpret their common ancestor as marine. According to Wägele's hypothesis, the Atlantasellidae, too, would have had to re-invade marine waters, despite this family occurring only in insular marine caves (Bermuda : Sket, 1979). The biogeographic data on this group are still too poor to be certain. Thus, Wägele's uncritical evaluation of the microcerberids as primitively freshwater cannot be supported by the data.

CONCLUSION

Wägele's groundpattern method is circular and nonscientific because it forsakes global corrobo-

ration of character distributions for *a priori* theories about phylogenetic descent. Phylogenetic trees constructed by Wägele's method are likely to be nonoptimal if they are evaluated cladistically using global parsimony. Wägele offers no strict algorithm to replace parsimony analysis, only a poorly characterised and subjective scheme of "argumentation." Groundpattern reconstruction methods cannot be recommended as a means to estimate phylogenies.

ACKNOWLEDGMENTS – I thank Drs R. Brusca, G. Edgecombe, and W. Ponder for providing many useful suggestions for improving earlier versions of this manuscript, and several anonymous reviewers for additional corrections. I am grateful to Dr N. Coineau for suggesting *Vie et Milieu* as a home for this paper. The Australian Museum Trust has graciously supported my phylogenetic research. Mr S. Ahyong and Ms D. Bray assisted with the preparation of the plates. This paper is a contribution of the Centre for Evolutionary Research at the Australian Museum.

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Reçu le 23 janvier 1996; received January 23, 1996
Accepté le 8 mars 1996; accepted March 8, 1996

VIE MILIEU, 1996, 46 (2) : 155-161

RECODING WIDESPREAD DISTRIBUTIONS IN GENERAL AREA CLADOGRAM CONSTRUCTION

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BIOGEOGRAPHY
METHODOLOGY
CLADISTICS

ABSTRACT. – A new procedure, dubbed "no assumption coding", is proposed for handling widespread distributions in general area cladogram construction. It is based on the observation that many taxa have similar widespread distributions, and these may in fact be areas of endemism rather than products of dispersal following prior speciation in smaller areas. When using widespread distributions as building blocks for general area cladogram construction most authors tend to cut these up into constituent smaller areas of endemism, and subsequently treat them variously under Assumptions 0, 1 or 2. Furthermore, current biogeographic practice allows areas to occupy only a single position in the general area cladogram, whereas the known history of biota dictates the possibility of various positions. To remedy both unwarranted limitations it is proposed to code widespread distributions differently from that of their constituent areas. This acknowledges the possibility that such widespread areas are areas of endemism originating from a different age than that of their constituent areas. It also acknowledges that different organisms may have smaller or larger areas of endemism, thus allowing for more generally applicable general area cladograms. The "no-assumption" coding procedure is demonstrated through a simple paper example involving four clades occurring in five areas. Current coding procedures and the new proposal are compared using three commonly practiced cladistic biogeography methods Component Analysis, Brooks Parsimony Analysis, and Three Area Statements. Results are compared using Page's (1995) TreeMap 1.0 program. "No assumption" coding improves fit between general area cladograms and taxon area cladograms.

BIOGÉOGRAPHIE
MÉTHODOLOGIE
CLADISTIQUE

RÉSUMÉ. – Une nouvelle procédure, appelée "no assumption coding", est proposée pour traiter des répartitions vastes lors de la construction de cladogrammes d'aires générales. Elle est basée sur l' observation selon laquelle plusieurs organismes présentent de vastes répartions similaires, et une telle répartition peut correspondre en fait à des aires d'endémisme plutôt qu'au résultat de phénomènes de dispersion. Lorsque l'on utilise des répartitions étendues dans la construction de cladogrammes d'aires générales, la plupart des auteurs les subdivisent en aires d'endémisme plus petites, et les traitent ensuite de manière variable sous les "Assumptions" 0, 1 ou 2. En outre, la pratique biogéographique courante n'autorise qu'une seule position pour les aires d'endémisme dans le cladogramme d'aires générales, tandis que l'histoire géologique nécessite la possibilité de plusieurs positions. Pour remédier à ces deux limitations, il est proposé de coder les répartitions étendues de manière différente par rapport aux aires constitutives. Cette procédure prend en compte la possibilité selon laquelle ces répartitions étendues sont des aires d'endémisme apparues à un âge différent de celui de l'apparition des aires constitutives. Elle admet aussi que des organismes différents peuvent présenter des aires d'endémisme plus petites ou plus grandes, permettant donc une meilleure utilisation des cladogrammes d'aires générales. La procédure "no assumption coding" est présentée dans un exemple simple artificiel à propos de quatre groupes d'organismes répartis selon cinq aires de distribution. Les procédures courantes de codage sont comparées à la nouvelle procédure par des méthodes biogéographiques communes : "Component Analysis", "Brooks Parsimony Analysis", et "Three Area Statement". Les résultats différents sont confrontés au programme TreeMap 1.0 (Page, 1995). La nouvelle procédure proposée améliore la correspondance entre les cladogrammes d'aires générales et les cladogrammes des organismes.

INTRODUCTION

Cladistic biogeography attempts to deduce relationships of areas of endemism by analyzing and combining area cladograms of different groups of organisms. If a single general area relationship is found this can then be employed for developing historical scenarios for individual organism groups.

Cladistic biogeography methods are still under development, with major approaches still emerging. Rivalling methodologies for which software is available include "Component Analysis" (Nelson and Platnick, 1981; Humphries and Parenti, 1986; Page, 1990), "Brooks' Parsimony Analysis" (BPA) (Brooks, 1981; Wiley, 1988), "Component Compatibility Analysis" (CCA) (Zandee and Roos, 1987), and "Three Area Statements" Analysis (TAS) (Nelson & Ladiges, 1991). Component Analysis attempts to find general patterns (general area cladograms) by seeking the congruent parts of individual taxon area cladograms, BPA and CCA by using parsimony to solve conflicting area relationships. TAS collects minimal statements of area relationships (three area relationships) from the taxon area cladograms and uses a parsimony algorithm to analyze the matrix of areas and statements.

All methodologies have pros and cons, and differ in their outcome especially when handling conflicting data. General area cladogram construction faces large numbers of such "problem" data. These are (1) terminal clade members distributed over two or more areas of endemism (widespread distributions), (2) areas not occupied by one or more of the clades under study (missing distributions), (3) areas occupied by two or more terminal members of a single clade (redundant distributions). Previous authors devised different solutions to deal with these problem data, all involving aprioristic manipulations of the original data : deleting redundancies (Rosen, 1978), "Assumptions 1, 2" (Nelson and Platnick, 1981; Platnick, 1981), "0" (Zandee and Roos, 1987), putting (various types of) question marks in the matrix (Wiley, 1988), and deleting widespread distributions (Kluge, 1988). There is cause for questioning the legitimacy of some or all of these manipulations in the process of general area cladogram construction, because all taxon distributions contribute to the end result. Objectivity dictates that manipulations should be avoided as far as possible, because individal taxon area cladograms are the raw data for the pattern analysis, and as such ought to be left untouched. Precisely for this reason Zandee & Roos (1987) devised their Assumption 0. However, although this seems reasonable, because the empirical data are used and there is no active manipulation involved like in Assumptions 1 and 2, it is flawed because it inherently assumes that the constituent areas share a taxon that failed to respond to vicariant events (also pointed out by Nelson and Ladiges, 1991; Humphries, 1992). This is an *a priori* assumption because the widespread distributions may also be the result of dispersal over existing barriers.

The superiority of cladistic biogeography over other methods such as similarity comparisons rests in the use of phylogenies as building blocks for general area cladogram construction. The use of inferred ancestral distributions will ensure that historical events are not obliterated by present day ecogeographic phenomena. However, most cladistic biogeography methods (including Component Analysis, BPA, and TAS) handle the empirical data (taxon area cladograms) in such a way that the resultant general area cladograms present only single relationships for the areas of endemism. This restriction is unwarranted, because existing knowledge of earth history (e.g. Hallam, 1994) points rather strongly towards different area relationships in various geological periods. Many (if not most) areas of endemism are composite, i.e. consist of fragments with very different historical relationships (e.g. Duffels & De Boer, 1990). If cladistic biogeography aims at constructing general area cladograms reflecting the historical relationships of areas of endemism, it should allow areas to have multiple relationships.

So far, only Brooks (1990) in his attempt to find a solution for the presence of redundant distributions employed different coding for the same area in different positions in the cladogram. Thus, he potentially solved both the problem of redundant distributions and the single presence of areas in the general area cladogram.

NO ASSUMPTION CODING

The purpose of the present note is to suggest a similar solution for the coding of widespread distributions. The terminology "widespread distributions" is an *a priori* assumption, because only after general area cladogram construction it may become apparent that certain distributions are the likely result of dispersal or have other causes. Different groups have different ways of dispersion (range extension without crossing barriers) and are affected differently by the abiotic environment and vicariant events. Thus, if general area cladograms are constructed from individual cladograms of different organism groups, it is the rule rather than the exception to find smaller and larger, partially or wholly overlapping areas of endemism. If the smallest areas are used as *the* areas of endemism, under the present methods, the (par-

tially) overlapping larger areas are automatically considered widespread distributions. This is unfair towards taxa with larger distributions, which would not possess proper areas of endemism themselves, only widespread distributions. If we employ the operational definition of "area of endemism" of Platnick (1991) and Morrone (1994), as "the congruent distributional limits of two or more species" (see also Harold & Mooi, 1994), many of the widespread distributions, such as the marine Indowest-Pacific or the Boreal-Arctic distributions, are areas of endemism, with many species of different organism groups inhabiting the same large area. Manipulating individual parts of these areas under Assumptions 0, 1 and 2 is not warranted. There is a simple solution to both the problem of widespread distributions and of multiple area relationships which involves recoding the areas of endemism : if two or more species (in practice many species) have the same "widespread" distribution, the area is given a name separate from that of its constituent smaller areas, and is treated in the analysis as a separate area. In the general area cladogram the "widespread" area and its constituent areas are thus considered independently and may find their place in different parts of it. If the "widespread" and constituent areas all become sister areas in the general area cladogram this is taken as evidence of shared history of all constituent areas; if they end up as para- or polyphyletic, then individual constituent areas have histories independent of the "widespread" areas. The recoding procedure is dubbed "no assumption" because it tries to accept the distributional data as they appear in the real world, without making use of assumptions 0, 1 and 2 as far as handling "widespread" distributions are concerned. Simply said : after recoding "widespread" distributions no longer occur in the analysis, and controversy over the way they need to be handled has disappeared. Recognition of both the constituent areas of endemism and the "widespread" areas of endemism involves a certain amount of conjecture about the extent of the area and the nature of its borders. Other than these – admittedly vexing – problems (*cf.* Harold & Mooi, 1994) the "no assumption" coding employs the same set of criteria for assignment of a taxon to an area of endemism.

METHODS

The following paper example was devised to demonstrate "no assumption" coding : four different organism groups (1-4) are distributed over five areas (A, B, C, D, and E) (*cf.* Figs. 1 A-D). In two groups the same widespread distribution (A+E) is found. The four area cladograms are

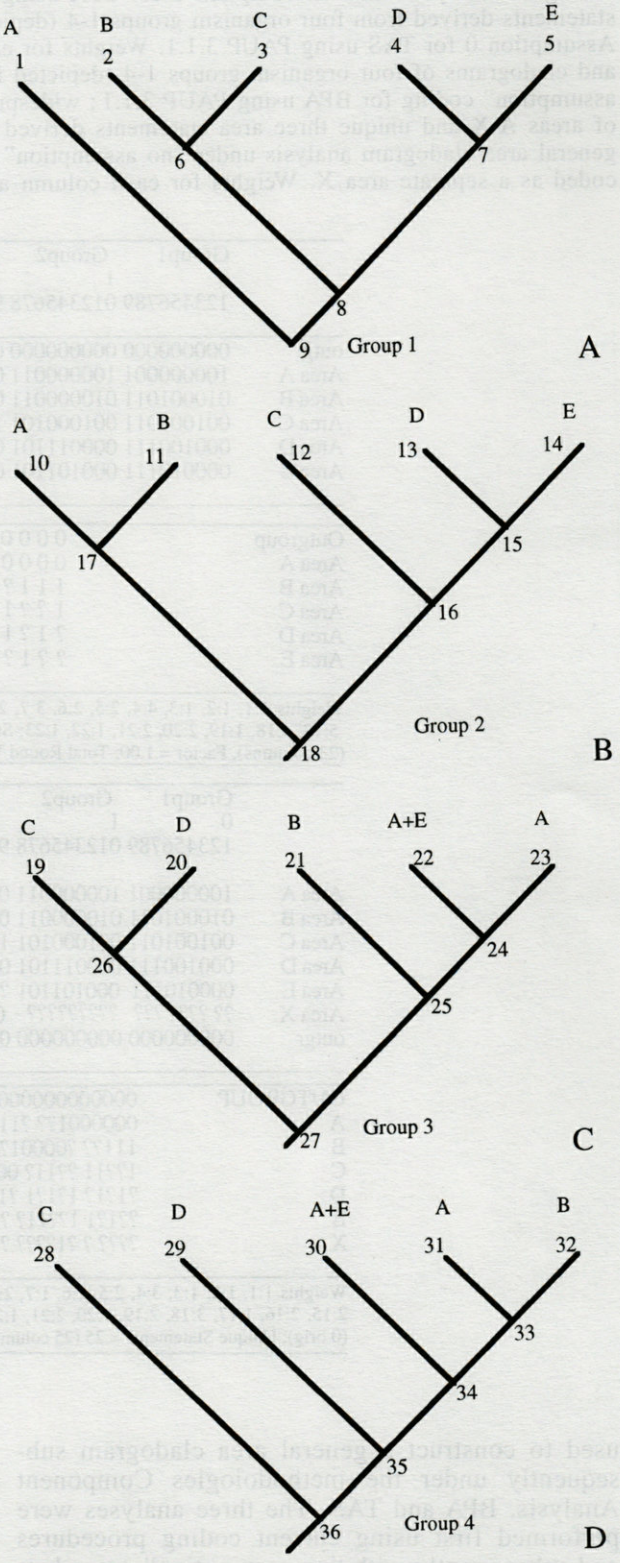

Fig. 1. – Area cladograms of four imaginary groups of organisms 1 (A), 2 (B), 3 (C) and 4 (D) distributed over 5 imaginary areas used as building blocks for general area cladogram construction using Component Analysis, BPA and TAS. Note that in the cladograms C and D one of the taxa is widespread over areas A and E.

Table I. – A, Matrix of areas A-E and taxa of four organism groups 1-4 (depicted in Fig. 1 A-D) for general area cladogram analysis under Assumption 0 for BPA using PAUP 3.1.1. B, Matrix of areas A-E and unique three area statements derived from four organism groups 1-4 (depicted in Fig. 1A-D) for general area cladogram analysis under Assumption 0 for TAS using PAUP 3.1.1. Weights for each column are provided in footnote. C, Matrix of areas A-X and cladograms of four organism groups 1-4 (depicted in Fig. 1A-D) for general area cladogram analysis under "no assumption" coding for BPA using PAUP 3.1.1; widespread distributions A+E coded as a separate area X. D, Matrix of areas A-X and unique three area statements derived from four organism groups 1-4 (depicted in Fig. 1A-D) for general area cladogram analysis under "no assumption" coding for TAS using PAUP 3.1.1; widespread distributions coded as a separate area X. Weights for each column are provided in footnote.

	Group1	Group2	Group3	Group4
	0	1	2	3
	123456789	012345678	901234567	890123456
outgr	000000000	000000000	000000000	000000000
Area A	100000001	100000011	000111101	001101111
Area B	010001011	010000011	001000101	000011111
Area C	001001011	001000101	100000011	100000001
Area D	000100111	000011101	010000011	010000011
Area E	000010111	000101101	000101101	001000111

A

Outgroup	000000000000000000000000
Area A	0000001 ???111 ??? 11 ??1??
Area B	111? ??000 01? ?11?1 ?1111?
Area C	1??1 1?? 11?000000? ?1??11
Area D	?1?1 ?1? 1?1?1?1?1?10000??1
Area E	??1? 111 ?11??1?11?1?1000

B

Weights 1:1, 1:2, 1:3, 4:4, 2:5, 2:6, 3:7, 2:8, 1:9, 2:10, 5:11, 2:12, 4:13, 1:14, 2:15, 3:16, 5:17, 4:18, 1:19, 2:20, 2:21, 1:22, 1:23; Statements = 52 (0 orig), Unique Statements = 23 (23 columns), Factor = 1.00; Total Round Weight = 52.

	Group1	Group2	Group 3	Group 4
	0	1	2	3
	123456789	012345678	901234567	890123456
Area A	100000001	100000011	000011101	000101111
Area B	010001011	010000011	001000101	000011111
Area C	001001011	001000101	100000011	100000001
Area D	000100111	000011101	010000011	010000011
Area E	000010111	000101101	?????????	???? ????
Area X	?? ???? ???	?????????	000101101	001000111
outgr	000000000	000000000	000000000	000000000

C

OUTGROUP	000000000000000000000000
A	0000001?? ?111? ?? ?11??1 ?1?
B	111?? ?00001??1 1? ?1?1111 1?
C	1??11 ??11? 0000000?? 1?? 1?1
D	?1?1? 1?1?1 ?1?1?1 10000? ??1
E	??1?1 1??11? ???? 1 ??? ??0 0??
X	???? ? ?1???? ?1?1 ?1?1 ?1? ?00

D

Weights 1:1, 1:2, 1:3, 3:4, 2:5, 2:6, 1:7, 2:8, 1:9, 2:10, 3:11, 1:12, 2:13, 1:14, 2:15, 2:16, 1:17, 3:18, 2:19, 1:20, 2:21, 1:22, 1:23, 1:24, 1:25; Statements = 40 (0 orig); Unique Statements = 25 (25 columns); Factor = 1.00; Total Round Weight = 40

used to construct a general area cladogram subsequently under the methodologies Component Analysis, BPA and TAS. The three analyses were performed first using current coding procedures and subsequently with "no-assumption" procedure involving the recoding of the A+E widespread distributions to a separate area coded X.

General area cladogram construction under Component Analysis was undertaken using the computer program Component 2.0 (Page, 1992). To allow a fair comparison with the other methods Assumption 0 was adopted. For the first run, the trees presented in Figs. 1A-D were fed in – using imaginary taxon names – and area cladograms were computed. They were subsequently combined using NNI (nearest neighbour interchange) and only minimum value trees were considered. For the second run in which widespread distributions A+E were coded as a separate sixth area "X", area E was treated as "missing" data in the clades of groups 3 an 4 (Figs. 1C and 1D). Area A was treated like areas B-C-D because it appears

as a separate area of endemism in cladograms 1C and 1D.

For BPA under Assumption 0 the areas x taxon matrix is presented in Table IA; missing areas are coded as "?". For BPA under "no-assumption" the taxon x areas matrix is presented in Table IC. As usual with BPA the matrix was given an outgroup vector of 0's to root the general area cladogram (Wiley, 1988). The computer program PAUP Macintosh version 3.1.1 (Swofford, 1993) (set to exhaustive search method) was used to generate the trees. The usual statistical parameters, consistency index and retention index (maximum value 1.000), were derived from the program for each tree.

Nelson & Ladiges (1992) developed a program 'TAS', which runs on a DOS operating system, but which has an option to port the output matrix to the MacIntosh version of PAUP. This was used to generate general areacladogram(s), by collecting only unique statements in the matrix; however, as recommended by the manual, columns were given weights according to the frequency in which they occurred in the original data (see Table IB and D).

Fit of the four taxon cladograms of groups 1-4 (Fig. 1A-D) on the general areacladograms generated under the two coding procedures was determined with Page's (1994, 1995) TreeMap 1.0 software for exploration of host-associate relationships (e.g. host-parasite or area-taxon). The options implemented in this program include determining the number of co-speciations of a host cladogram and an associate cladogram. If host cladograms are considered analogous to general area cladograms and associate cladograms to taxon area cladograms, the program can be used to test the fit of these and compare various general areacladograms with each other.

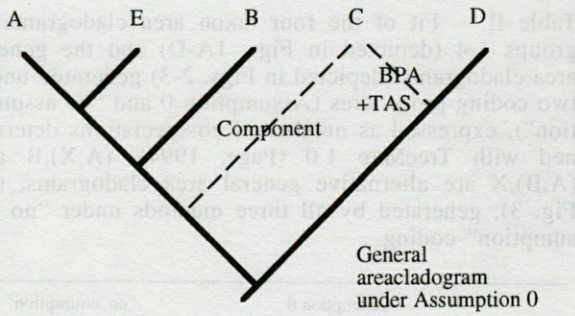

Fig. 2. – General area cladogram resulting from analysis by Component 2.0, BPA and TAS under Assumption 0 using the four area cladograms depicted in Fig. 1 (matrices for BPA and TAS given in Table I C). Note that the solutions differ for area C (dashed lines), and that A and E are sister areas.

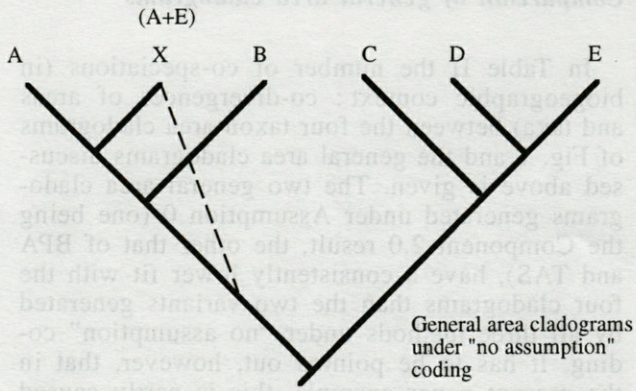

Fig. 3. – General area cladograms resulting from Component Analysis, BPA and TAS under "no assumption" coding (recoding widespread distribution A+E as X) using the four area cladograms depicted in Fig. 1 (matrices for BPA and TAS given in Table I C). All three methods yielded the same two trees differing in the position of area X relative to A and B (dashed line). Note that in both solutions E has sister group relationships with both A (or AB) and D.

RESULTS

The Component Analysis-Assumption 0 result is a single tree (minimum value 25) (Fig. 2). BPA Assumption 0 likewise resulted in a single shortest tree with a length of 44 steps, a consistency index 0.818 and a retention index of 0.615 (Fig. 2). This tree differs from the Component Analysis result in the position of area C. In both cases general area cladogram construction has forced the component A-E as the only sister area relationship for those two areas. The TAS result was identical to that of BPA, but due to the character weighting the tree had more steps (72), lower consistency (0.722), but the same retention index (0.615).

The Component "no assumption" analysis (Fig. 3) resulted in two trees (minimum value 18), differing in the relative position of areas A, B and X. The BPA "no assumption" analysis resulted in two equally short trees, each with a length of 40 steps, a consistency index of 0.900 and a retention index of 0.733. They were identical to the trees generated under Component. The TAS result is identical also, with trees of 49 steps length, 0.816 consistency index and 0.775 retention index. If we acknowledge that area "X" consists of areas A and E, we can now see that in the general area cladograms area E has two different sistergroup relationships, with area A and with area D.

Table II. – Fit of the four taxon area cladograms of groups 1-4 (depicted in Figs. 1A-D) and the general area cladograms (depicted in Figs. 2-3) generated under two coding procedures (Assumption 0 and "no assumption"), expressed as number of co-speciations determined with TreeMap 1.0 (Page, 1994). (A,X),B and (A,B),X are alternative general area cladograms, (cf. Fig. 3), generated by all three methods under "no assumption" coding.

	Assumption 0		"no assumption"	
	Component	BPA/TAS	(A,X),B	(A,B),X
Group 1	2	2	3	3
Group 2	2	3	4	4
Group 3	2	3	4	3
Group 4	2	2	3	3

Comparison of general area cladograms

In Table II the number of co-speciations (in biogeographic context : co-divergences of areas and taxa) between the four taxon area cladograms of Fig. 1 and the general area cladograms discussed above is given. The two general area cladograms generated under Assumption 0 (one being the Component 2.0 result, the other that of BPA and TAS), have a consistently lower fit with the four cladograms than the two variants generated by all three methods under "no assumption" coding. It has to be pointed out, however, that in the present paper example, this is partly caused by the increased number of internal nodes, which increases the chances of "co-divergences". It can not as yet be concluded that general area cladograms in the real world would have a better fit when obtained using this coding method. A further positive result is that the "no assumption" coding has removed the conflicting results of the three methods.

DISCUSSION

The "no-assumption" recoding procedure gives full credit to the original "raw" data and avoids *a priori* manipulations involved in cutting up wide spread distributions into smaller constituent areas. The "no assumption" recoding procedure opposes the point raised by Axelius (1991). She attempted to demonstrate that in the case of overlapping areas of endemism it is best to split them up into constituent areas and treat these separately in the analysis. Technically, Axelius' example is flawed because one of the constituent areas she uses, i.e. the overlap of the two areas of endemism, apparently has no taxa of its own, and thus is not an area of endemism (see also Harold & Mooi, 1994). Platnick (1991) also supports the idea of using the smallest area units possible, even if they are not areas of endemism. However, I disagree strongly : although biogeography is about areas, not about taxa, the basic units of biogeography are areas of endemism. Cutting these up on the basis of arbitrary criteria, other than the congruent distributions of two or more organisms, is questionable.

Confronted with large numbers of problem data as can be expected in real world general area cladogram construction, use of Assumption 2 (Humphries, 1992) will very probably lead to unmanageable numbers of alternative cladograms to be processed. The current version of COMPONENT, version 2.0, is not equipped to handle these (*cf.* restrictions indicated in the manual) and also TAS does not implement Assumption 2 (although it theoretically can be done by hand). Recoding redundant and widespread areas in the sense of Brooks (1990) and as here proposed appears to be a better way to confront these practical problems because of their tendency to smoothen out conflicting area relationships.

ACKNOWLEDGMENTS – Dr R.D.M. Page generously made his software TreeMap 1.0 available through anonymous FTP. Professor Fred R. Schram is thanked for allowing the use of his copy of COMPONENT 2.0. The copy of PAUP 3.1.1 used here is licensed to Dr J. Parnell, Dublin. Dr Eduardo Hajdu assisted me with the use of the program COMPONENT 2.0 as well as with his copy of TAS. Drs Fred R. Schram, Wallie H. de Weerdt, Ronald Sluys, Harry A. ten Hove and E. Hajdu are thanked for their valuable suggestions for improvement.

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Reçu le 2 janvier 1996 ; received January 2, 1996
Accepté le 26 avril 1996 ; accepted April 26, 1996

VIE MILIEU, 1996, 46 (2) : 163-169

LIFE-HISTORIES, SPECIATION, AND BIODIVERSITY IN MEDITERRANEAN PROSOBRANCH GASTROPODS

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SPECIATION
BIODIVERSITY
LARVAL ECOLOGY
MEDITERRANEAN
PALEOCLIMATE

ABSTRACT. – Marine gastropod molluscs are a very suitable group to study life-histories and speciation processes related to temporal and spatial patterns of biodiversity. Several developmental strategies have been adopted by marine prosobranch gastropods, that can fall into two fundamental categories : 1) planktotrophic development, with larvae feeding on plankton ; 2) non-planktotrophic development, with larvae that reach metamorphosis without feeding on plankton and usually spend less time or no time at all in the plankton. Presently, the Northeast Atlantic prosobranch fauna includes a large number of pairs of sibling species differing mainly or only in developmental strategy. A speciation model involving loss of planktotrophy as a leading factor, has been proposed to explain this pattern. Heterochronic changes during morphogenesis are considered the basis for such speciation events involving shifting of larval strategies, and epigenetic plasticity seems to explain some of the observed patterns rather well. In these cases environmental factors may have been responsible for "switching off" the pelagic larval phase in specific conditions, with a selection against planktotrophs. Restricted areas, higher predation rate, changes in food availability and temperature, are considered as some of the main selecting factors. The Mediterranean Sea proved to be a good laboratory to test the model. Comparison of palaeontological data, distribution patterns, molecular (allozyme) dating of some cladogenetic events, address the very Recent history of the basin. Quaternary palaeoclimatic fluctuations are very good candidates as responsible for having produced conditions (restricted areas, confinement, higher predation rate, fluctuating food availability etc.) unsuitable for the planktotrophs.

SPÉCIATION
BIODIVERSITÉ
ÉCOLOGIE LARVAIRE
MÉDITERRANÉE
PALÉOCLIMAT

RÉSUMÉ. – Les Mollusques Gastéropodes marins représentent un des groupes les plus appropriés à l'étude des cycles biologiques et des processus de spéciation, liés aux modèles temporels et spatiaux de biodiversité. Les Gastéropodes Prosobranches ont adopté plusieurs stratégies de développement, que l'on peut classer dans deux catégories : 1) planctotrophes, avec des larves qui se nourrissent de plancton, et 2) non-planctotrophes, avec des larves qui ne se nourrissent pas de plancton et qui ne sont pas planctoniques, ou qui le sont pour une période très brève. Dans la faune de l'Atlantique Nord-Est de nombreux couples d'espèces de Prosobranches ne diffèrent entre elles que par les stratégies de développement. Un modèle de spéciation, avec perte de la planctotrophie comme facteur guide, a été proposé pour expliquer ce phénomène. Des modifications hétérochroniques pendant la morphogenèse sont considérées comme la base de ces déplacements dans les stratégies larvaires et des phénomènes de spéciation qui en résultent, un certain degré de plasticité épigénétique peut aussi expliquer la dynamique du phénomène. Des facteurs environnementaux jouent un rôle décisif dans la suppression de la phase planctotrophe, avec la sélection négative des larves planctotrophes. Les principaux facteurs sont reconnaissables dans la limitation des aires, la prédation élevée, les changements de température et de sources alimentaires. La Mer Méditerranée se présente comme un bon laboratoire pour vérifier ce modèle. La comparaison des données paléontologiques, des types de distribution, des datations moléculaires (allozymiques) des divergences cladogénétiques, nous amène à considérer l'histoire récente du bassin. Les fluctuations paléoclimatiques du Quaternaire représentent les causes les plus probables des conditions environnementales (aires limitées, confinement, prédation élevée et fluctuation des ressources alimentaires, etc.) négatives pour les planctotrophes.

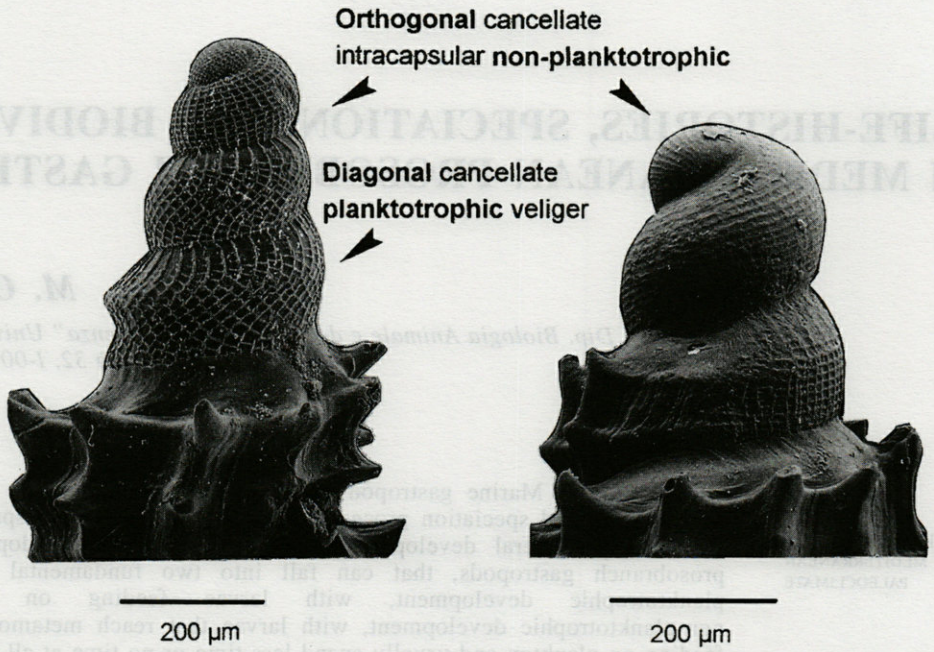

Fig. 1. – Protoconchs of two prosobranch gastropods showing differences in the sculpture between a planktotrophic and a non-planktotrophic embryonic/larval shell. A, *Raphitoma hystrix* De Cristofori & Jan, from the Upper Pliocene of Tabiano (Italy) : 3 1/2 whorls, planktotrophic. B, *Raphitoma pseudohystrix* Sykes, from Central Tyrrhenian Sea – 80 m : 1 1/2 whorls, non-planktotrophic. Scale bar = 200 µm.

INTRODUCTION

Biodiversity is the product of a series of processes operating over time and space. In the past, attention has been mostly paid to the spatial patterns of biodiveristy. In several marine environments, the recent advances in taxonomy resulted in discovering a high number of sibling/cryptic species. This fact produced figures of diversity three to five times greater than previously recognised (Knowlton & Jackson, 1994), and we are probably looking only at the tip of an iceberg in most cases (Knowlton, 1993). More recently, the problem of a deeper understanding of dynamic processes producing biodiversity has been raised. Such processes have important components operating over a temporal scale, and speciation plays obviously a central role. Presently, interest is growing into aspects of speciation related to adaptation. The life histories of the involved organisms play an important role in the understanding of the speciation mechanisms. Particularly, larval ecology (long vs. short/absent pelagic life) exerts a remarkable influence on the life history of a species, especially as concerns their dispersal capability, the possibility and the extent of gene flow between populations, as well as the extinction/speciation rate (Mileikovsky, 1971; Scheltema, 1972, 1977; Shuto, 1974; Valentine and Jablonski, 1986; but see also Hedgecock, 1986).

Marine gastropod molluscs are a very suitable group to this aim. Likewise most of the marine invertebrates (see e.g. Jablonski & Lutz, 1983; Strathmann, 1978 a, 1978 b, 1985), several developmental strategies have been adopted by the marine prosobranchs. Regardless the uptake of dissolved organic material as an additional source of energy (Manahan, 1990; Jaeckle & Manahan, 1989), they can fall into two fundamental categories.

[P] planktotrophic development, with larvae feeding on plankton, spending a relatively long time in the planktonic stage;

[NP] non-planktotrophic development : in the most part lecithotrophic (but including also direct development, brooding, etc.) : larvae, if present (lecithotrophic), have at their disposal a more or less large yolk supply, reach metamorphosis without feeding on plankton and usually spend less time or no time at all in the plankton.

Features of embryonic/larval shells (protoconchs) are powerful tools to identify the mode of development of each individual (Fig. 1); if the protoconch is preserved in the adults, their larval development can be inferred from characteristics of the sculpture and by comparison of the dimensions (Thorson, 1950; Jablonski & Lutz, 1980). The developmental type of specimens in fossil material (Fig. 1A) can be also defined, when the protoconchs are preserved. It is a rare possibiliy in the Animal kingdom, that allows to study this biological feature along a temporal dimension.

SIBLING SPECIES

A recent study scored the presence in the Northeast Atlantic prosobranch fauna of a large number of pairs of sibling/cryptic "species" differing mainly or only in the developmental strategy (Oliverio, 1994 a). This world wide phenomenon (Hoagland and Robertson, 1988) has a particular relevance in this area. A particularly large number of such pairs are concentrated in the Mediterranean basin (Table I). In a few cases, the actual status of some such pairs of morphs (whether they might be considered as sibling species, or not) has still not been defined conclusively, although most of the "species" are currently accepted as such by European malacologists (e.g., Sabelli *et al.*, 1990-1992; see also Hoagland and Robertson, 1988; Bouchet, 1989).

The existence of sibling species, differing only or mainly in their larval development witnesses in favour of a model of speciation involving loss of planktotrophy as a leading factor (Oliverio, 1991, 1996). In such a scenario the models of speciation, related in some way to larval ecology, are synthesised as follows :

I. Speciation within groups with planktotrophic development. Speciation usually occurs at the edges of the ancestral species range (Hansen, 1978; Shuto, 1974); often a peripatric model (Mayr, 1982) could explain the speciation events, notwithstanding the alleged homeostatic effect of the larval dispersal.

II. Speciation within groups with non-planktotrophic development. Usually because of the reduction or even absence of gene flow between populations (low dispersal capability), speciation appears like a classic allopatric event, and in some conditions, radiation may be favoured because of the isolation of the demes.

III. Speciation associated with the loss of planktotrophy (Oliverio, 1991, 1996). The mechanism of this type of speciation involves the modification of larval development. Environmental factors can be responsible for switching off the pelagic larval phase in specific conditions that select against planktotrophs. Restricted areas, higher predation rate, changes in food availability, etc., can be considered as the main factors (Strathmann, 1978 a, b).

Heterochrony is suggested to be an important prerequisite for evolutionary developmental transitions; it can explain the (presumably intraspecific) variation observed in some cases. Changes in timing (speed and sequence) of the developmental pathways underlie many aspects of organismal diversity (Gould, 1977; McKinney, 1988; Raff *et al.*, 1990). Yet, little is known about the mechanisms ruling heterochronic variations (Blackstone and Buss, 1993; Parks *et al.*, 1993), and only recently theoretical models for the reaction norm are being tested (Gavrilets and Scheiner, 1993 a and b). Heterochronic changes in genes operating during oogenesis can result in changes (even dramatic) in the developmental pathway. According to Strathmann *et al.* (1992) heterochrony can account for at least the initial transition to non feeding larval development. Such epigenetic plasticity does not require the acceptance of a polymorphism and fits rather well with an approach of the problem under an "Alernative adaptation" perspective (West-Eberhard, 1986; see also Smith-Gill, 1983). Alternative developmental phenotypes produced by heterochrony can provide the basis for speciation.

The analysis of the distribution ranges of the "forms" within each pair provides useful insight for the comprehension of the mechanisms of Speciation III. An increasing dominance of the NP mode going eastward in the Mediterranean has been observed. Taking the Sicily Channel area as the boundary, exclusively eastern and western distribution are automatically defined. Prevalently eastern and western distribution are those of the species ranging slightly over the boundary, but with the main ranges centred East and West of the Channel, respectively. Out of the list in Table 1,21 NP vs. 7 P taxa have their prevalent or exclusive distribution in the Eastern basin; 9 NP vs. 20 P are prevalently or exclusively found in the Western basin.

THE WORKING HYPOTHESIS

During the last epochs, several geological events (e.g. closure of Tethyan and Atlantic connections, reopening of Gibraltar and the entry of cold water from the Atlantic in the Pleistocene) were important factors contributing to the modification of the Mediterranean faunas in the period from Miocene to Pleistocene (see Di Geronimo, 1990, for a comprehensive review). It can be considered that one or more of the Late Tertiary to Quaternary geological events that characterised Mediterranean history, could have operated on a number of species, at different times, providing speciation opportunities. This is partly confirmed by the analysis of the evolution of larval development in some prosobranch lineages in the Mediterranean area (Oliverio, 1994 a; Oliverio and Sabelli, unpublished). The paleontological data set indicates a clear trend toward the loss of planktotrophy in those lineages, with P NP transitions located in few points along the temporal scale. Paleoclimatic fluctuations also produced important changes on Mediterranean faunal assemblages, and in very recent times. Levels of genetic

Table I. – Pairs of "morphs" and their distribution. A = Atlantic; M = Mediterranean; W = Western Mediterranean (W to the Sicily Channel); E = Eastern Mediterranean (E to the Sicily Channel); * = Localized, endemic to (...). **Bold capitals** indicate the preferential distribution.

planktotrophic	distribution		non-planktotrophic
Alvania rudis (Philippi, 1844)	WE	WE	*A. litoralis* (Nordsieck F., 1972)
Alvania cimex (Linné, 1758)	W	WE	*A. mamillata* Risso, 1826
Alvania testae (Aradas & Maggiore, 1844)	WE	WE	*A. subsoluta* (Aradas, 1847)
		WE	*A. elegantissima* (Monterosato, 1875)
Alvania cancellata (Da Costa, 1778)	WE	W	*A. hirta* Monterosato, 1844
Alvania discors (Allan, 1818)	WE	WE	*A. lineata* Risso, 1826 group
Rissoa labiosa (Montagu, 1803)	AWE	E*(Gabes)	*R. paradoxa* (Monterosato, 1844)
		AE	*R. membranacea* (Adams, 1800)
Rissoa radiata Philippi, 1836	W	WE	*R. munda* (Monterosato, 1884)
Rissoa guerini Recluz, 1846	WE	WE	*R. lia* (Monterosato, 1844)
Rissoa ventricosa Desmarest, 1814	WE	WE	*R. variabilis* (Von Muehlfeldt, 1824)
R. splendida Eichwald, 1830	E		
Rissoa pulchella Philippi, 1836	WE	E	*R. marginata* Michaud, 1832
Rissoa monodonta Philippi, 1836	WE	E	*R. auriformis* Pallary, 1904
Rissoa auriscalpium Linné, 1758	WE	W*(Tyrrh.)	*R. italiensis* Verdun, 1985
		E	*R. rodhensis* Varduin, 1985
Rissoa similis Scacchi, 1836	WE	E	*R. scurra* (Monterosato, 1918)
Rissoa violacea Desmarest, 1814	WE	E	*R.* sp.
Vitreolina curva (Monterosato, 1974) group	WE	E	*V. levantina* Oliverio *et al.*, 1994
Columbella adansoni Menke, 1853	A	AM	*C. rustica* (Linné, 1758)
Nassarius circumcinctus (Adams, 1851)	WE	E	*N. gibbosulus* (Linné, 1758)
Nassarius caboverdensis Rolàn, 1984	A	M	*N. ferrusaci* Payraudeau, 1826
Mangelia rugulosa (Philippi, 1844)	W	E	*"Mangiliella" barashi* Aartsen & Fehr-de Wal, 1978
Mangelia paciniana (Calcara, 1839)	W	E	*"Mangiliella" sandrii* (Brusina, 1865)
Mangelia costulata (Blainville, 1826)	WE	E*Gabès	*"Mangiliella" pallaryi* (Nordsieck, 1977)
Mangelia scabrida (Monterosato, 1890)	WE	E	*"Mangiliella" secreta* Aartsen & Fehr-de Wal, 1978
Bela nebula (Montagu, 1803)	WE	E	*"Fehria" taprurensis* (Pallary, 1904)
Bela nana (Scacchi, 1836)	WE	E	*"Fehria" zenetouae* Aartsen, 1988
Raphitoma laviae (Philippi, 1844)	WE	WE	*"Philbertia" philberti* (Michaud, 1829)
Raphitoma echinata (Brocchi, 1814)	WE	WE	*"Philbertia" horrida* (Monterosato, 1844)
Headropleura sp.	A	M	*H. septangularis* (Montagu, 1803)

divergence, based on allozymic data from a few case-studies (Oliverio, 1994a, b, 1996; Munksgaard, 1990) address relatively recent events of separation of the entities within each pair.

The Atlantic neogastropod *Columbella adansoni* (with planktotrophic development) is separated from the mainly Mediterranean *Columbella rustica* (its sibling/sister with non-planktotrophic development) at a genetic distance of ca D = 0.4; this level allows dating (Nei, 1987) the cladogenetic event at ca. 2 MY bP. Noteworthy, this estimate indicates the period following the onset of the glaciations and their southward extension (Tunnell and Douglas, 1983; Thunnell *et al.*, 1984). Confinement of the Mediterranean basin during cool phases probably supported the speciation event. The present distribution pattern recalls the glacial southward faunal shifts (Taviani *et al.*, 1991), with boreal species moving from North, and thermophilic species (as *C. adansoni* appears to be, according to its tropical-subtropical range) being often pushed southward along the African coasts (Oliverio, 1994 a, 1995).

In the North Sea the *Rissoa labiosa* [P]/*R. membranacea* [NP] pair has been studied by Munksgaard (1990). She scored evidence of genetic isolation in sympatric populations of the two species. The genetic distance between them was ca. D = 0.056 dating the speciation to ca. 200-250 000 years bP.

Much lower levels have been scored (Oliverio, 1994 b) in the populations of two rissoid

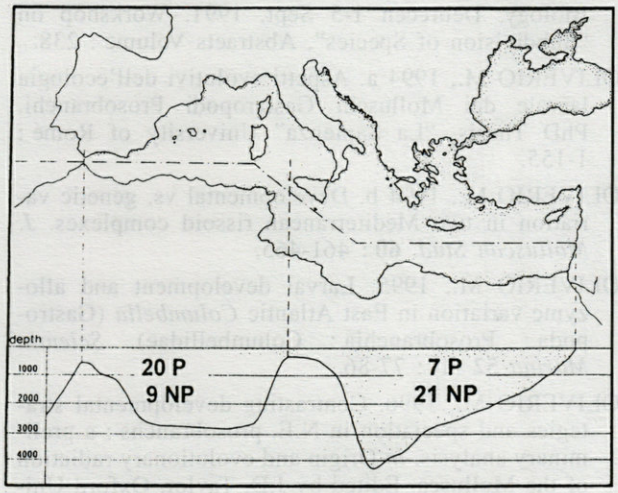

Fig. 2. – Schematic representation of the Mediterranean basin showing the figures of P Vs. NP with distributions exclusive or prevalent in one of the two subbasins (Table I).

complexes (*Rissoa auriscalpium* and *R. violacea*). Such figures indicate (comparing Aegean [NP] and Tyrrhenian [P] populations in both cases) times of divergence of 5-6.000 years and 40-50.000 years, respectively.

Quaternary paleoclimatic fluctuations are normally regarded as the main factor having affected land and freshwater biodiversity in the Mediterranean region (see e.g. La Greca, 1984). Their effects also on the marine assemblages are probably not fully acknowledged.

The peculiar physiognomy of the Mediterranean Sea (Fig. 2) played an important role during that time. The Mediterranean Sea is in fact, a concentration basin separated from the main ocean by the Gibraltar threshold. Internally it consist of two main sub-basins (eastern and western) also separated by a sill (the Siculo-Tunisian channel). During glacial periods the Mediterranean vs. the Atlantic, and the eastern vs. the western basin, underwent a strong isolation due to hydrographic factors. Inversion of water flows at both sills (Gibraltar and the Siculo-Tunisian one) contributed perhaps seasonally to such confinement, and sea level lowering produced reductions of the Sicily Channel up to three quarter width (Bethoux, 1979, 1984). Such conditions promoted the main factors suggested to counter select the planktotrophic larvae (Strathmann, 1978 a, b) : fluctuations in the energy (food) input, restricted areas, higher predatory pressure.

The model proposed is a working hypothesis, which needs to be carefully tested on the basis of research focusing on taxonomy, palaeobiogeography, morphology and physiology. Comparisons with other areas (Baltic Sea, Red Sea, Arabian Gulf) and/or animal groups (Annelida and Echinodermata should prove to be good fields : Guérin and Kerambrun, 1984; Levin *et al.*, 1991; Strathmann *et al.*, 1992) could help in detecting if there are common patterns of the model in animals with similar life strategies (Hasgprunar *et al.*, 1995).

The most correct approach to the study of biodiversity must focus (also) on the dynamic processes operating and having operated to produce present patterns. Speciation processes reveal obviously important aspects, and their study must include the definition of the adaptive factors in the speciation events. Speciation is presently even more seen as a non-random event, not only a by product of geographic separation and/or of genetic drift. Selection and adaptation probably play more important roles than commonly suggested and the analysis of aspects related to life-histories, connected with speciation will yield important results in the definition of the underlying mechanisms of speciation. This will allow to asses a more general model for Speciation III, relating environmental and life-histories changes, and will result in a better understanding of the processes producing biodiversity in the ocean.

ACKNOWLEDGMENTS – This topic has been presented by the author at the Euroconference "Oceanography : Biodiversity and Production in the oceans" (San Feliu de Guixol, 3-7 May 1994), and useful discussions held there improved this paper. A grant by the European Science Foundation to attend the meeting is gratefully acknowledged.

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Reçu le 7 juin 1994 ; received June 7, 1994
Accepté le 12 mai 1995 ; accepted May 12, 1995

VIE MILIEU, 1996, 46 (2) : 171-181

PHYLOGENÈSE ET CONVERGENCE CHEZ LES ISOPODES TERRESTRES

Phylogeny and convergence within the terrestrial isopods

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CRUSTACEA
ISOPODA
ONISCIDEA
CONVERGENCE
ADAPTATION
PHYLOGENÈSE
CLASSIFICATION CLADISTIQUE

RÉSUMÉ. – L'analyse cladistique des principaux groupes d'Oniscidea a été entreprise dans le but de montrer la monophylie de ce sous-ordre. L'histoire évolutive des différents traits morphologiques est exposée et leur signification est discutée afin de discerner correctement les synapomorphies, et d'éviter les erreurs d'interprétation dues aux évolutions convergentes. La succession des dichotomies qui apparaissent dans la phylogenèse des Oniscidea est présentée et son utilité pour une nouvelle classification de ce sous-ordre, basée sur des données cladistiques, est soulignée. On distingue une super-section Orthogonopoda comme groupe frère des Diplochaeta.

CRUSTACEA
ISOPODA
ONISCIDEA
CONVERGENCE
ADAPTATION
PHYLOGENY
CLADISTIC CLASSIFICATION

ABSTRACT. – A cladistic analysis of the main groups of the suborder Oniscidea was performed in order to check for their monophyletic origin. The paper deals with the evolutionary history of various morphological traits and its significance for both recognition of synapomorphies and the avoidance of interpretative errors due to convergent evolution. The successive phylogenetic dichotomies of the main Oniscidea groups are shown and their utility for a new classification system is discussed. A super section Orthogonopoda, as a sister group of Diplochaeta is recognised.

1. INTRODUCTION

Les Oniscidea – sous-ordre le plus riche en espèces de l'ordre des Isopoda – représente le seul groupe de Crustacés qui s'est adapté en quasi-totalité au milieu terrestre. Ce passage à la vie terrestre, avec les modifications morphologiques et physiologiques complexes qu'il a entraînées, s'est réalisé graduellement à l'intérieur de plusieurs lignées parallèles ce qui fait que les relations de parenté entre les divers groupes et l'argumentation de la monophylie du sous-ordre posent certains problèmes du fait de la difficulté à déceler les véritables synapomorphies. Pour contribuer à l'éclaircissement de ces problèmes nous avons effectué une première analyse phylogénétique (Tabacaru et Danielopol, 1996). Le cladogramme le plus parcimonieux a été réalisé en utilisant des algorithmes heuristiques (méthodes de Wagner et de Camin-Sokal) et exacts (méthode « branch and bound » de D. Penny) existant dans les logiciels Phylip 3.5c et Paup 3.0. Les données ont été comparées avec un cladogramme construit à la main ; l'ensemble des résultats obtenus étant totalement congruent : un seul arbre à 43 pas, pleinement résolu à partir de 43 caractères (25 autapomorphies et 18 synapomorphies).

Pour réaliser cette analyse phylogénétique un matériel abondant a été examiné ; nous avons étudié les caractères déjà utilisés dans la systématique des Isopodes et cherché de nouveaux caractères significatifs. Il convient de préciser que, dans l'examen des séquences de transformation des caractères, nous n'avons pas rencontré de difficultés pour reconnaître leur polarité, c'est-à-dire pour distinguer à différents niveaux l'état plésiomorphe et l'état apomorphe. En effet, nous avons toujours tenu compte de la comparaison extra-groupe et de la corrélation des caractères en considérant la direction évidente de certaines transformations liées au passage des Isopodes à la vie terrestre. Cependant, des difficultés résultent des homoplasies, c'est-à-dire de nombreuses structures similaires qui ne proviennent pas de l'héritage d'un ancêtre commun. On peut affirmer que la plus grande difficulté dans l'analyse cla-

distique des Oniscidea réside dans ces évolutions convergentes. D'ailleurs Mayr (1972) affirme qu'en effet tous les auteurs qui ont essayé d'évaluer les caractères de taxa élevés ont conclu que le phénomène de convergence « is the most troublesome problem ».

Le but de cette note est de présenter l'analyse qui a permis de déceler les évènements uniques permettant de prouver la monophylie des Oniscidea et de reconnaître les grands groupes de ce sous-ordre ainsi que leur filiation.

2. LE PROBLÈME DES HOMOPLASIES

Si l'on considère les deux catégories d'homoplasie, c'est-à-dire la réversion et la convergence, on peut affirmer que dans la phylogenèse des Isopodes terrestres, la réversion est un phénomène nettement moins fréquent que la convergence sous sa forme particulière, le parallélisme.

2.1. Les réversions

On rencontre souvent le cas de réversions représentées par la disparition de structures d'où résulte une situation similaire à l'état initial qui précédait l'apparition de ces structures. Mais ces caractères négatifs, ne posent pas en général de problèmes car l'analyse corrélative des caractères dans leur séquence évolutive permet de reconnaître qu'il s'agit de réversions et non de plésiomorphies. Quand ces caractères sont en congruence avec les caractères positifs synapomorphiques il y a une très grande probabilité pour qu'ils soient aussi des synapomorphies. Ainsi, par exemple, l'absence des rétinacles sur l'endite du maxillipède a été interprétée par Brusca et Wilson (1991) comme une plésiomorphie ; mais, en considérant que les rétinacles existent chez la grande majorité des Isopodes aquatiques, nous sommes d'avis que leur absence chez tous les Isopdes terrestres est une réduction (réversion) qui représente une synapomorphie des Oniscidea.

Un cas typique de réversion est la multiplication aberrante du nombre des pénicilles du lobe interne de la maxillule à l'intérieur de la famille des Eubelidae, car nous considérons comme une synapomorphie de tous les Crinocheta, y compris les Eubelidae primitifs, la réduction du nombre des pénicilles de 3 à 2.

Il existe très peu de cas où l'analyse de l'évolution des caractères ne conduit pas à une conclusion. Par ex. la bifurcation de l'apophyse génitale chez certains Crinocheta (Halophilosciidae) a été interprétée comme un reste de la dualité primitive (plésiomorphie) par Kesselyak et par Vandel et comme secondaire (réversion), due à la coaptation avec les endopodites 1, par Maccagno et par Verhoeff (cf. Vandel, 1962). Mais, au niveau de l'analyse des taxa élevés, de tels caractères interviennent assez peu en général.

Nous avons rencontré une seule réversion qui a conduit à d'importantes interprétations erronées : le retour à la vie aquatique entraînant une série de modifications morphologiques (augmentation de la taille des exopodites des pléopodes, allongement des antennes 1 et 2 et parfois multiplication du nombre d'articles du flagelle antennaire, allongement du palpe du maxillipède, nombreuses brosses sur la maxille). Dans la section des Crinocheta on connaît 2 cas, *Haloniscus searlei* et *Haloniscus anophthalmus*, mais les auteurs sont unanimes à considérer qu'il s'agit d'une adaptation secondaire (Vandel, 1973 ; Taiti, Ferrara et Iliffe, 1995). Par contre, le cas des espèces troglobies, à mode de vie aquatique, appartenant à la section des Synocheta (*Typhlotricholigioides aquaticus, Cantabroniscus primitivus, Titanethes albus, Mexiconiscus laevis, Bureschia bulgarica, Balearonethes sesrodesanus, Thailandoniscus annae*) a conduit à supposer une origine indépendante de cette section. Nous avons démontré (Tabacaru, 1993 ; Tabacaru et Danielopol, 1996) qu'il s'agit aussi d'un retour secondaire à la vie aquatique.

2.2. Les évolutions parallèles

La fréquence des convergences et des parallélismes dans l'évolution des Isopodes a été remarquée depuis longtemps. Racovitza (1910), considérant que la « classification naturelle », phylogénétique, est le but suprême de la taxonomie, conclut qu'il « est donc nécessaire d'examiner les caractères taxonomiques du groupe du point de vue de leur histoire et de leur signification phylogénétique ». Il affirme que les caractères doivent être groupés en caractères de filiation et caractères d'adaptation et que l'on doit les hiérarchiser suivant leur ancienneté relative. Il distingue à la suite de Abel : a, des caractères de parallélisme (dus à l'évolution parallèle d'organes homologues) et b, des caractères de convergence (dus à l'évolution convergente d'organes non homologues). Il affirme que les cas de parallélisme et de convergence sont plus fréquents qu'on ne pense et que beaucoup de caractères employés en systématique sont dus à l'évolution parallèle ou convergente et non des caractères de filiation, ces derniers, seuls, pouvant servir à établir des classifications naturelles.

Dans ses travaux sur les Isopodes terrestres, Vandel a fréquemment remarqué des évolutions parallèles et a considéré qu'elles révèlent l'existence de potentialités morphogènes et évolutives

propres à l'ensemble du groupe. Selon Vandel (1943), dans un groupe donné, le parallélisme des lignées phylétiques qui le constituent, est le signe de leur origine commune. D'ailleurs, Brundin (1966, *in* Goujet *et al.*, 1988), affirme également que le parallélisme est un phénomène très répandu qui a un rapport évident avec le degré de proximité d'ascendance, mais qu'il ne peut être une preuve d'une relation fraternelle. Donc, c'est à juste titre, que l'on considère la convergence et le parallélisme comme des concepts identiques du point de vue de l'analyse cladistique (Darlu et Tassy, 1993) ; les deux phénomènes représentent des similitudes réalisées indépendamment, et qui, donc, ne sont pas dues à une ascendance directe et ne permettent pas la construction d'un taxon monophylétique. Néanmoins, nous reconnaissons que dans le cas d'un parallélisme très prononcé, le « rampant parallelism » de Sluys (1989), les caractères respectifs peuvent apporter des informations parfois utiles dans l'analyse phylogénétique des taxons moins élevés (famille, tribu, genre, espèce).

La non-congruence de certains caractères, observée au cours de l'édification du cladogramme, donc la supposition de se trouver en présence de convergences, nous a déterminés, conformément à la méthodologie hennigienne, à réexaminer les caractères concernés et à envisager des solutions différentes :

a. Suite à l'examen des caractères *a priori*, nous avons éliminé certaines synapomorphies proposées par d'autres auteurs et qui étaient fondées sur des erreurs d'observation (pléopode 1 mâle de *Calabozoa* et de Crinocheta ; pléopode 1 mâle des Tylidae et Mesoniscidae ; appareil respiratoire des Tylidae, Mesoniscidae et Ligiidae) ; le réexamen des caractères a conduit à la conclusion que certaines synapomorphies proposées sont fondées sur des ressemblances superficielles et non sur de véritables similitudes (antennules des Ligiidae, des Mesoniscidae et des Tylidae ; uropodes des Tylidae et des Actaeciidae ; apophyses génitales des Tylidae et des Mesoniscidae ; endopodite 1 mâle de Synocheta et Crinocheta).

b. Nous avons souvent trouvé des évolutions parallèles d'organes homologues, situation nommée « homoiologie » d'après Plate (Hennig, 1982 ; Sudhaus et Rehfeld, 1992), mais, dans la plupart des cas, l'examen du matériel nous a permis de reconnaître qu'il s'agit d'apomorphies distinctes par certains détails de structure et surtout par leur valeur fonctionnelle. Un exemple typique : chez 2 groupes distincts d'Isopodes, les Valvifera et les Tylomorpha, les uropodes ont évolué d'une manière convergente : par le développement et l'aplatissement du protopodite, ils deviennent 2 opercules attachés au bord latéral du pléon et rabattus comme des volets sur la face ventrale du pléon. Cette similitude, interprétée comme la preuve d'une parenté (Vandel, 1943, 1960) ou comme une convergence (Schmalfuss, 1989), dissimule en réalité 2 autapomorphies remarquables. Chez les Valvifera, les uropodes fonctionnent comme des opercules allongés qui protègent les pléopodes tandis que chez les Tylomorpha, ils s'emboîtent avec un septum transversal et séparent l'espace respiratoire de l'espace anal.

c. Un nouvel examen des caractères nous a conduits aussi à reconnaitre qu'une similitude morphologique accentuée et considérée comme synapomorphe, représente en réalité un développement convergent qui masque une vraie synapomorphie réalisée par une dichotomie antérieure (l'aspect convergent de l'apophyse génitale des Synocheta et des Crinocheta a fait passer inaperçue la synapomorphie représentée par la soudure des 2 apophyses génitales apparue au niveau de la séparation des Orthogonopoda).

d. Lorsqu'un caractère qui n'existe pas chez les formes primitives d'un groupe, ou n'existe seulement à l'état rudimentaire se manifeste chez tous les représentants évolués de ce groupe, et que sa présence est associée à d'autres caractères qui représentent des synapomorphies, nous considérons qu'il s'agit d'une tendance qui doit être interprêtée comme une synapomorphie. Les exemples sont nombreux : réduction du palpe du maxillipède par rapport au basis du même palpe chez les Oniscidea ; captation par la fonction sexuelle du 1er pléopode mâle des Synocheta ; apparition sur les exopodites des pléopodes d'organes respiratoires à stigmates dorsaux chez les Crinocheta ; disparition des rangées longitudinales parallèles d'écailles sur les péréiopodes 6 et 7 des Crinocheta.

e. Nous avons éliminé les similitudes qui représentent de multiples évolutions convergentes apparues à des niveaux hiérarchiques très différents. C'est le cas de la volvation, terme introduit par Verhoeff pour désigner le moyen de défense par l'enroulement en boule chez certains Isopodes aquatiques et surtout chez les Isopodes terrestres chez lesquels elle a peut-être aussi un rôle de protection contre la dessication du corps. Dans le sous-ordre des Oniscidea, la volvation n'existe pas chez les Diplocheta et les Microcheta, donc elle n'est pas un caractère hérité de l'ancêtre marin. Elle existe chez les Tylomorpha, les Buddelundiellidae parmi les Synocheta, chez de nombreuses familles ou des genres de différentes familles de la section des Crinocheta. La volvation, avec ses multiples systèmes d'engrenage, ne fournit donc pas d'information utile pour reconstituer la filiation des grands groupes d'Oniscidea et elle doit être utilisée avec circonspection, car ainsi que l'a remarqué Dalens (1990), dans de nombreux cas, les différentes manifestations de la volvation ne représentent en fait que des parallélismes évolutifs situés à des stades d'évolution

identiques et non des affinités phylogénétiques réelles. D'ailleurs, de Lattin (1961) considère que les multiples transformations parallèles qui ont conduit indépendamment à la naissance du type volvationnel dans différentes familles d'Isopodes doivent être dues surtout à des complexes géniques différents et non à une même combinaison de gènes.

f. Enfin, nous avons éliminé certaines similitudes concernant des caractères négatifs notamment l'absence de traits rudimentaires qui persistent seulement chez les Diplocheta et les Isopodes aquatiques primitifs et qui ont disparu indépendamment dans toutes les autres lignées (sillon occipital, vestige de l'articulation du 1er thoracomère avec le céphalon, squame, rudiment de l'exopodite de l'antenne).

3. ÉVOLUTION DES ONISCIDEA – SYNAPOMORPHIES ET CONVERGENCES

L'étude de la phylogenèse des Isopodes terrestres permet de reconnaître 3 aspects principaux : 1, une évolution régressive par laquelle des structures primitives héritées de l'ancêtre marin se simplifient ou disparaissent; 2, une évolution adaptative qui conditionne la conquête des milieux terrestres de plus en plus secs; 3, une évolution diversifiante qui a comme conséquence le grand nombre de genres et d'espèces du sous-ordre des Oniscidea. Ces 3 aspects se déroulent en interdépendance car certaines simplifications représentent une condition préalable pour la réalisation de structures capables d'accomplir une nouvelle fonction dans le milieu terrestre. Ainsi par ex., la fusion des 2 apophyses génitales a permis la réalisation de coaptations complexes existant entre l'unique apophyse et la 1e paire de pléopodes qui, d'une part assurent la rapidité et la précision de la transmission du sperme, nécessaire aux formes des milieux secs (Legrand, 1946) et, d'autre part, ont déclenché la grande diversification générique et spécifique de la structure du pléopode 1 des Synocheta et des Crinocheta.

Pour discerner les synapomorphies et éviter les erreurs d'interprétation dues aux évolutions convergentes, nous avons examiné les transformations de différents caractères en analysant surtout la signification de chaque similitude. Nous n'avons pas envisagé ici les multiples aspects de l'évolution diversifiante caractéristique du niveau générique ou spécifique (ornementation tergale, caractères tégumentaires, etc.), mais nous avons suivi l'évolution des caractères sexuels mâles importants pour la diversification des grands groupes.

3.1. La régression des structures primitives

Comme l'a affirmé Vandel à maintes reprises depuis ses travaux de 1943, l'histoire des Isopodes terrestres est en grande partie une évolution régressive et simplificatrice qui se déroule d'une manière parallèle, mais asynchrone, dans toutes les lignées. Certaines transformations régressives qui se manifestent chez tous les Isopodes terrestres ou chez tous les représentants d'un groupe, en concordance avec des synapomorphies positives sont, selon toute probabilité, également des caractères synapomorphiques. Nous n'avons pas pris en considération dans notre analyse les traits régressifs comme la réduction de la taille ou de la pigmentation qui sont variables au sein d'une espèce ou même d'une population, en fonction des conditions du milieu.

3.1.1. Fusion des plaques coxales 2-7 avec les péréionites

Chez les Isopodes primitifs (Phreatoicidea, Asellota), la coxa des péréiopodes est encore fonctionnelle tandis que chez la plupart des Isopodes elle est devenue marginale, se substituant au bord primitif sous la forme d'une plaque distincte, articulée avec la région latérale du péréionite, nommée par Racovitza euépimère. Mais ce processus se continuant de façon indépendante dans diverses lignées d'Isopodes, a abouti à la fusion plus ou moins complète avec le péréionite (pleurépimère). Dans le sous-ordre des Oniscidea, le stade de plaque nettement individualisée et articulée au péréionite existe seulement chez les Tylomorpha, représentant un caractère plésiomorphe hérité de l'ancêtre marin. Aucun représentant des Ligiamorpha ne possède de telles plaques coxales; seuls les Stenoniscidae ont encore des plaques coxales très étroites marquées par une ligne de suture. La fusion des plaques coxales avec les péréionites représente une synapomorphie des Ligiamorpha.

3.1.2. Régression de l'appareil oculaire

Les Isopodes terrestres les plus primitifs, les Diplocheta, ont, comme leur ancêtre marin, un appareil oculaire constitué d'un très grand nombre d'ommatidies (500-800 chez *Ligia*, 110-120 chez *Ligidium*). Chez les autres Oniscidea, ce nombre diminue considérablement. Les Tylomorpha en ont 20-50; chez certains Crinocheta primitifs le nombre est encore élevé (*Scyphax ornata* 150-200, *Actaecia euchroa* 150), mais la grande majorité des espèces de cette section en ont un nombre réduit, de 40 à 5, et la réduction aboutit même parfois à une seule ommatidie (*Benthanops fulva*, *Eluma purpurascens*). Globalement, dans le sous-ordre des Oniscidea, la réduction du nombre d'ommatidies est plus constante dans la section

des Synocheta : espèces à 3 ommatidies ; espèces à 1 ommatidie ; espèces anophthalmes. Nous considérons cette importante réduction des yeux (au maximum 3 ommatidies) comme une synapomorphie du groupe Microcheta-Synocheta. Précisons que dans toutes les sections, les espèces troglobies, endogées, mirmécophiles ou termitophiles, ont un appareil oculaire régressé voire absent, ce phénomène étant lié à la vie obscuricole.

3.1.3. Réduction de l'antennule

Elle a été considérée par Vandel (1943, 1960) comme le seul caractère propre à tous les Isopodes terrestres. En effet, chez les Oniscidea, l'antennule présente au plus 3 articles, ce qui constitue sans doute une synapomorphie. La réduction de l'antennule est extrême chez les Tylomorpha avec 1 seul article (on a même considéré longtemps que cet appendice manque chez *Helleria*). Elle présente 3 articles chez la plupart des représentants des Ligiamorpha ; la réduction du 3^{e} article est un phénomène qui se produit indépendamment dans différentes lignées.

3.1.4. Réduction du nombre d'articles du flagelle antennaire

L'antenne des Oniscidea est caractérisée par la réduction graduelle du nombre des articles du flagelle en rapport avec l'adaptation progressive au milieu terrestre. Chez les Diplocheta, le nombre d'articles est encore relativement élevé (*Ligia* 10-38, *Ligidium* 11-14). Il se réduit brusquement chez les Tylomorpha (*Tylos* 3-4, *Helleria* 2). Les Microcheta ont un flagelle de 7-8 articles. Les représentants de grande taille des Synocheta en ont un nombre assez grand (*Alpioniscus* 9-13, *Titanethes* 10-14), mais la plupart des espèces en ont seulement 3 ou 4. Précisons que chez les Microcheta et les Synocheta les articles sont tronconiques, non rétrécis à la base. Il y a en outre une tendance à l'effacement de la limite entre articles du flagelle des Synocheta. Le nombre d'articles des Crinocheta primitifs est aussi variable (*Olibrinus* 8-18, *Adoniscus* 4-7, Scyphacidae 4). Par contre ce nombre devient constant chez les Crinocheta évolués : 3 (Philosciidae, Halophilosciidae, Oniscidae et certains représentants des Scleropactidae et Eubelidae) ou 2 articles (la plupart des familles). Etant donné les nombreux parallélismes dans la réduction du nombre des articles du flagelle antennaire, ce phénomène, malgré sa direction évolutive évidente, ne peut être utilisé dans l'étude de la filiation des grands groupes d'Oniscidea, mais tout au plus pour décrire leur diversification (Crinocheta surtout).

3.1.5. Disparition du palpe mandibulaire et de la *pars molaris*

Le palpe mandibulaire manque chez tous les Oniscidea et on peut supposer qu'il a disparu chez leur ancêtre et qu'il s'agit donc d'une synapomorphie. Mais le palpe a disparu d'une manière convergente chez beaucoup d'Isopodes aquatiques (Keuphyliidae, Lynseiidae, Valvifera excepté *Holognathus*, *Calabozoa*, Bopyridae). Nous trouvons justifié l'affirmation de Wägele (1944) selon laquelle ce caractère négatif ne peut prouver une parenté phylétique entre *Calabozoa* et les Oniscidea en l'absence de caractères constructifs synapomorphiques. L'adaptation de l'appareil buccal à une nourriture plus sèche s'exprime dans la conformation de la mandibule par le développement de la *pars incisiva* et la réduction de la *pars molaris*. Ce caractère représente une autapomorphie des Crinocheta.

3.1.6. Fusion des endites de la maxille

Chez les Isopodes, la maxille comprend 3 endites distincts pourvus de longues tiges ciliées. Chez tous les Oniscidea la maxille est devenue une lame étroite bilobée à son apex ; le rudiment très étroit d'un lobe intermédiaire persiste seulement chez *Ligioides intermedius* entre les 2 lobes. Certains Isopodes aquatiques carnivores ou parasites ont aussi la maxille réduite, mais il s'agit sans doute d'un phénomène de convergence. La conformation très simple et constante de la maxille des Oniscidea représente une des synapomorphies les plus importantes du groupe.

3.1.7. Réduction du palpe du maxillipède

Parmi les synapomorphies des Oniscidea, Wägele (1989) mentionne le « basipodite plus long que le palpe ». En effet, en comparant le maxillipède d'un Isopode aquatique (palpe à 5 articles nettement plus long que le basipodite) avec celui d'une espèce de Crinocheta (palpe très court à 3 articles), la différence est évidente. Cependant, chez certaines espèces de *Ligia* le palpe est bien développé avec 5 articles. On peut donc seulement parler d'une tendance à la réduction du palpe se manifestant dans toutes les sections d'Oniscidea.

3.2. Evolution des structures adaptatives au milieu terrestre

Les nombreuses stratégies morphologiques ayant permis aux Isopodes de conquérir les différentes niches du milieu terrestre sont particulièrement informatives pour la différenciation des familles, des genres et des espèces, mais nous examinons ici les modifications morphologiques

essentielles qui ont permis le passage à la vie terrestre et qui donnent des informations utiles pour prouver la monophylie des Oniscidea et surtout pour distinguer les grands groupes constituant ce sous-ordre.

L'étude de l'adaptation graduelle au milieu terrestre sous l'aspect écophysiologique a fait l'objet de très nombreux travaux parmi lesquels les synthèses de Wieser (1984) et de Warburg (1987) permettent de comprendre la signification majeure de certaines transformations morphologiques.

3.2.1. Le système de circulation de l'eau sur la surface du corps

Le caractère le plus important apparu avec le passage à la vie terrestre est sans doute le système qui permet la circulation de l'eau sur la surface du corps. Ce système maintient l'humidification des téguments en assurant les fonctions essentielles : respiration, excrétion, thermorégulation. Verhoeff a découvert ce système « Wasserleitungssystem » en 1917 et soupçonné son importance ; grâce aux travaux de Hoese (1981, 1982), on a reconnu que ce caractère existe chez tous les Isopodes terrestres et il représente donc une synapomorphie de ce groupe (Schmalfuss, 1989 ; Wägele, 1989). Hoese (1981) distingue deux types de fonctionnement de ce système : « le type-*Ligia* » et le « type-*Porcellio* ». Du point de vue morphologique, le « type-*Ligia* » est caractérisé par la présence de rangées longitudinales parallèles d'écailles sur les faces caudale du péréiopode 6 (excepté sur le basipodite) et rostrale du péréiopode 7 (au moins sur le basipodite), permettant l'absorption de l'eau du substrat par capillarité. Nous avons vérifié la présence de ces rangées d'écailles chez *Tylos, Helleria, Ligia, Ligidium, Mesoniscus* et chez de très nombreux représentants de Synocheta. Précisons que chez *Cantabroniscus primitivus* (Trichoniscide aquatique), on peut encore remarquer sur le basipodite de P7 les traces de ces rangées d'écailles. On a aussi signalé la présence de rangées d'écailles chez certains Crinocheta primitifs, mais tous les Crinocheta évolués possèdent le système d'humidification du corps de « type-*Porcellio* » dans lequel les rangées d'écailles des péréiopodes n'existent plus. Nous considérons la tendance à la disparition des rangées parallèles d'écailles sur P6 et P7 comme une synapomorphie des Crinocheta.

3.2.2. Evolution du marsupium

La constitution de la poche incubatrice, le marsupium, présente de remarquables particularités propres aux différents groupes d'Oniscidea. Tout d'abord, remarquons une particularité n'existant que chez *Tylos* et *Helleria* et qui représente donc une autapomorphie des Tylomorpha : la cavité marsupiale se prolonge à l'intérieur du pléon par un long sac interne (Mead, 1973).

Une particularité propre aux représentants des Crinocheta et qui constitue une adaptation aux milieux de vie plus secs, est la présence de cotylédons dans le marsupium, appendices qui prennent naissance sur la face ventrale des péréionites. En rapport avec les deux types de système de circulation d'eau à la surface du corps, Hoese et Janssen (1989) considèrent deux types de marsupiums : le « type amphibie » qui est ouvert aux extrémités antérieure et postérieure, permettant la circulation de l'eau par capilarité, et le « type terrestre » fermé, caractérisé par la présence d'un liquide sécrété par les cotylédons. Ce denier type représente une autapomorphie des Crinocheta.

3.2.3. Evolution de l'appareil respiratoire

Chez les Oniscidea primitifs, les endopodites des pléopodes, protégés par les exopodites et recouverts continuellement par une pellicule d'eau grâce au système de circulation de l'eau sur la surface du corps, ont la fonction d'organes respiratoires branchiaux. Avec l'adaptation graduelle aux milieux de plus en plus secs, se développent dans les exopodites des organes respiratoires aériens sous la forme d'un système de plis ouverts ou de tubes. L'apparition de ces organes respiratoires dans les exopodites se manifeste d'une manière convergente chez les Tylomorpha et les Crinocheta. Mais l'étude comparative permet de préciser qu'il s'agit de 2 autapomorphies. La différence la plus évidente est que chez les Tylomorpha les exopodites 2-5 renferment des organes respiratoires à stigmates ventraux tandis que chez les Crinocheta apparaissent des organes respiratoires à stigmates dorsaux.

3.2.4. Evolution de l'estomac

L'examen de la structure complexe de l'estomac chez un grand nombre d'espèces d'Isopodes aquatiques et terrestres nous a conduit à remarquer la grande variation dans la constitution de cet organe chez les Oniscidea ; la large gamme alimentaire dans les différents groupes de ces derniers pourrait l'expliquer (Wieser, 1984 ; Strus *et al.*, 1995). L'étude des particularités structurales de l'estomac des Oniscidea montre l'existence de différences même au niveau des espèces.

Chez les Oniscidea primitifs l'estomac présente une structure générale proche de celle de certains Isopodes aquatiques. Par rapport à la conformation de l'estomac des différents groupes, la structure de la valvule dorsale oesophagienne nommée par Vandel (1943) « superomedianum » est caractéristique ; cette valvule offre l'aspect d'une lan-

guette très allongée chez les Microcheta alors qu'elle est courte et semi-circulaire chez les Synocheta.

L'adaptation à la vie dans le milieu terrestre, notamment la consommation d'une nourriture plus sèche, se manifeste chez les Crinocheta surtout par la modification de la conformation de l'estomac et par le développement du typhlosole. En ce qui concerne l'estomac, on remarque une simplification et en même temps une spécialisation. Nous considérons comme une autapomorphie des Crinocheta l'absence de la valvule dorsale oesophagienne ce qui permet l'ingestion de particules plus grandes.

3.3. Evolution des caractères sexuels mâles

Chez les Oniscidea, l'évolution diversifiante la plus importante concerne les caractères sexuels mâles, mais précisons que la différenciation sexuelle des péréiopodes et l'apparition d'organes glandulo-pilifères se situent au niveau spécifique ou au plus générique. Pour l'analyse phylogénétique des niveaux hiérarchiques plus élevés, l'évolution de l'apophyse génitale ainsi que celle des 2 premières paires de pléopodes ont fourni des informations essentielles, malgré certains caractères convergents.

3.3.1. Evolution des apophyses génitales.

On considère (Wägele, 1989; Wilson, 1991; Brusca et Wilson, 1991) que la position primitive des apophyses génitales se trouve sur le côté médian de la coxa; à la suite de la tendance à une migration vers la ligne médiane, celles-ci se rapprochent en restant, dans une 1ere phase, en connexion avec les coxa, puis, dans une phase plus évoluée, s'insèrent sur le bord caudal du péréionite et aboutissent à une fusion totale. Cette évolution se déroule d'une manière convergente dans différentes lignées; on trouve une seule apophyse médiane chez *Calabozoa*, les Arcturidae (Valvifera), certains Gnathidae et surtout chez les Oniscidea supérieurs. Dans le sous-ordre des Oniscidea la conformation la plus primitive, certainement la plus proche de celle qui a existé chez l'ancêtre marin, persiste encore chez les Diplocheta avec 2 apophyses génitales longues, parallèles, à base commune, s'insérant sur la membrane articulaire qui relie le péréion au pléon. Leur évolution a suivi 2 directions nettement différentes : chez les Tylomorpha, elles ont complètement disparu, chez les Ligiamorpha, elles ont évolué vers la fusion totale.

Wägele (1989) considère la réduction des apophyses génitales comme une synapomorphie des Mesoniscidae et des Tylidae, mais les recherches récentes (Erhard, 1995; Tabacaru et Danielopol, 1996) conduisent à la conclusion qu'il s'agit d'un aspect convergent. En effet, chez les Tylidae les apophyses génitales ont disparu et les 2 canaux déférents débouchent éloignés l'un de l'autre, tandis que chez *Mesoniscus*, les 2 apophyses sont réduites, avec une soudure médiane. On peut donc parler de 2 autapomorphies. Parallèlement, Schmalfuss, 1989; Wägele, 1989 et Erhard 1995 soutiennent que la fusion médiane des apophyses est une synapomorphie des Synocheta et des Crinocheta. Nous voyons plutôt une convergence dans la similitude des apophyses génitales des Synocheta et des Crinocheta car leur structure et leur rapport avec la 1ere paire de pléopodes sont nettement différents (Legrand, 1946; Vandel, 1957). Nous considérons la soudure médiane des 2 apophyses comme une synapomorphie de l'ensemble Microcheta-Synocheta-Crinocheta. A partir de l'ancêtre à apophyses génitales soudées ont dérivé 3 structures différentes : apophyses réduites, à orifices rapprochés produisant un seul spermatophore par accolement des 2 spermatophores initiaux (Microcheta); apophyses complètement fusionnées (y compris les canaux déférents), avec un seul orifice, donc un seul spermatophore (Synocheta); apophyses fusionnées mais à canaux déférents distincts, donc 2 orifices et 2 spermatophores séparés (Crinocheta).

3.3.2. Evolution de l'endopodite du pléopode 2

En général, chez les Isopodes l'endopodite du pléopode 2 joue le rôle d'organe copulateur. La forme la plus primitive de différenciation est représentée par la séparation, du côté médian de la lame endopodiale, d'un appendice digitiforme, l'*appendix masculina* qui a un rôle dans l'accouplement. Grüner (1993) affirme que chez *Calabozoa*, les Asellota et les Oniscidea, l'*appendix masculina* manque car l'ensemble de l'endopodite est modifié en organe copulateur. Vandel (1943) et Wägele (1989) considèrent que la lame endopodiale des Oniscidea est réduite à l'article basal de l'*appendix*. Parmi les Isopodes aquatiques, il existe des cas représentant sans doute des convergences qui indiquent la possibilité d'une telle transformation : *appendix masculina* à insertion terminale (*Arubolana*); réduction de la lame endopodiale et insertion terminale de l'*appendix* (Serolidae). Une évolution en sens inverse, comme le suppose Schmalfuss (1989), c'est-à-dire l'élargissement de l'article basal de l'*appendix masculina* pour devenir lame natatoire nous semble improbable. Tabacaru et Danielopol (1996) arrivent à la même conclusion que Erhard (1995) quant à l'importance d'une modification de l'endopodite 2 du mâle dans l'évolution des Oniscidea : chez les Oniscidea primitifs (Tylomorpha, Diplocheta) l'endopodite est articulé en continuité du basipodite ou obliquement sur celui-ci et forme

un angle entre son article basal et le second article, tandis que chez l'ensemble Microcheta-Synocheta-Crinocheta, l'endopodite est perpendiculaire au basipodite sans former d'angle entre les articles basal et 2.

3.3.3. Evolution de la première paire de pléopodes

Dans l'ordre des Isopoda, quelques groupes aquatiques (Janiroidea, Arcturidae, *Calabozoa*) et les Oniscidea évolués présentent une modification des pléopodes mâles pour participer à la fonction sexuelle. Il s'agit d'évolutions indépendantes qui aboutissent à des structures complètement différentes.

Chez les Oniscidea l'évolution des pléopodes 1 a suivi 2 directions divergentes, comme celle des apophyses génitales : dans les 2 sexes des Tylomorpha, exopodite et endopodite ont complètement disparu et il n'existe qu'un reste du basipodite ; chez les Ligiamorpha, les pléopodes 1 mâles, encadrant les 2 ou l'unique apophyse(s) génitale(s), ont subi une différenciation progressive (surtout l'endopodite) en vue de faciliter le transport du sperme vers les organes copulateurs formés par l'endopodite des pléopodes 2. Les pléopodes 1 des Mesoniscidae sont réduits comme chez les Tylidae (Vandel, 1943 ; Legrand, 1946 ; Wägele, 1989). En effet, exopodites et endopodites des Mesoniscidae sont bien développés mais ne présentent pas de différenciations sexuelles (Gruner et Tabacaru, 1963). Chez les espèces primitives de *Ligia* qui appartiennent aux Diplocheta, la différenciation sexuelle est limitée au développement plus prononcé de l'angle distal interne de l'endopodite du mâle, mais chez tous les autres représentants, il existe un faisceau de macrochètes dans l'angle distal interne de l'exopodite et de l'endopodite.

Wägele (1989) et Erhard (1995) ont considéré comme une synapomorphie des Synocheta et des Crinocheta l'allongement de l'endopodite 1 du mâle. A notre avis, la modification de l'endopodite 1 mâle pour la fonction sexuelle des Synocheta et des Crinocheta représente deux phénomènes indépendants qui ne peuvent constituer une synapomorphie. Chez les formes primitives de Synocheta, l'endopodite est une simple lame étroite parfois très petite comme chez la femelle (*Brackenridgia, Typhlotricholigioides*) ; l'endopodite de la majorité des Synocheta porte une tige ciliée plus ou moins développée ou un bâtonnet ; chez les Synocheta évolués (Trichoniscini, Haplophthalminae, Buddelundiellidae), les endopodites sont biarticulés avec un article distal en forme de lame de couteau devenant ainsi des organes paracopulateurs. Les endopodites des Crinocheta sont allongés, robustes et pourvus d'une gouttière spermatique ; les 2 orifices de l'apophyse génitale débouchent dans cette gouttière. Cette coaptation représente une autapomorphie des Crinocheta. La ressemblance entre l'endopodite des Crinocheta et l'exopodite de *Calabozoa* ne prouve aucune relation de parenté.

4. DISCUSSION ET CONCLUSIONS

La discussion et les conclusions portent sur la phylogenèse et la classification des Oniscidea.

En concluant que le petit Isopode *Calabozoa* ne représente pas un Isopode terrestre adapté à la vie aquatique (ni un groupe frère), que les Tylidae ne peuvent être rattachés aux Valvifera et que le mode de vie aquatique de certaines espèces troglobies de Synocheta ne prouve pas l'origine indépendante de cette section, les synapomorphies de tous les Isopodes terrestres attestent de la monophylie des Oniscidea. Nous considérons les synapomorphies suivantes : 1. apparition du système de circulation d'un liquide à la surface du corps ; 2. présence de soies-écailles sur la surface dorsale du corps ; 3. endopodite du pléopode 2 mâle entièrement transformé en stylet copulateur ; 4. antennule constituée au plus de 3 articles ; 5. maxille réduite à une pièce unitaire bilobée ; 6. mandibule sans palpe ; 7. endite du maxillipède sans rétinacle ; 8. forte tendance à la réduction du palpe du maxillipède par rapport au basis.

La recherche des autapomorphies nous a permis de distinguer et de définir les grands groupes monophylétiques des Oniscidea. Nous considérons ainsi les Diplocheta au sens restreint de Schmalfuss (1989), comprenant seulement les Ligiidae et non au sens de Wägele (1989, 1994) qui y inclut les Mesoniscidae et les Tylidae, ni dans l'ancien sens, c'est-à-dire Diplocheta Vandel, 1957 = Protophora archaica Verhoeff, 1917 = Ligiidae + Mesoniscidae. Les autapomorphies permettent de séparer les Mesoniscidae dans une section à part, les Microcheta Schmalfuss, 1989 qui représentent le groupe frère des Synocheta. Par contre, les Crinocheta, au sens de Schmalfuss (1989) représentent en même temps un groupe paraphylétique (car il ne comprend pas les Olibrinae) et polyphylétique (par l'inclusion des Tylidae). Précisons que les Olibrinidae présentent les autapomorphies des Crinocheta et non celles des Synocheta et que les autapomorphies des Tylidae ne permettent de les inclure ni dans les Diplocheta, ni dans les Crinocheta.

Nous avons donc considéré 5 groupes monophylétiques, Tylidae, Diplocheta (Ligiidae), Microcheta (Mesoniscidae), Synocheta et Crinocheta, qui représentent les taxons terminaux dans notre analyse.

En suivant la conception initiale de Vandel (1943, 1960) qui a isolé les Tylidae des autres Isopodes terrestres, certains auteurs (Bowman et Abele, 1982; Holdich *et al.*, 1984; Brusca et Wilson, 1991) ont divisé le sous-ordre des Oniscidea en deux infra-ordres : Tylomorpha Vandel, 1943 et Ligiamorpha Vandel, 1943. Par contre, Schmalfuss (1989), Wägele (1989, 1994) et Erhard (1995) considèrent que la division des Oniscidea en Tylomorpha et Ligiamorpha n'est pas justifiée. Schmalfuss (1989) et Erhard (1995) trouvent plutôt des arguments pour la monophylie de tous les «non-Ligiidae», c'est-à-dire pour une opposition des Ligiidae à tous les autres Oniscidea.

Notre analyse cladistique nous a conduit à la conclusion selon laquelle deux lignées distinctes sont issues de l'ancêtre commun des Oniscidea Tylomorpha et Ligiamorpha. Ils sont donc groupes frères mais ont évolué depuis longtemps indépendamment car cette dichotomie est à la base de la diversification du sous-ordre dans l'histoire des différents caractères (plaques coxales, uropodes, apophyses génitales, pléopode 1 mâle, appareil respiratoire, poche incubatrice).

Les Tylomorpha (une seule famille, Tylidae, avec 2 genres, *Tylos* et *Helleria*) montrent un mélange de nombreuses plésiomorphies avec des apomorphies représentant soit des caractères de haute spécialisation (séparation entre l'espace respiratoire et l'espace anal; organes respiratoires à stigmates ventraux; sac interne prolongeant la poche incubatrice; antennule réduite à un seul article), soit des caractères à valeur restrictive, c'est-à-dire qui ont nettement limité la possibilité de diversification du groupe (disparition des apophyses génitales; disparition des pléopodes 1). En ce qui concerne les plésiomorphies, rappelons que les Tylidae sont les seuls Oniscidea chez lesquels persistent les plaques coxales nettement individualisées car la soudure des plaques coxales avec les péréionites représente une synapomorphie des Ligiamorpha. La grande dissymétrie numérique existant entre les Tylomorpha et les Ligiamorpha s'explique par le fait que *Tylos* et *Helleria* ne représentent que des relictes d'une longue évolution dont les étapes intermédiaires ont disparu.

La dichotomie suivante essentielle dans la phylogenèse des Oniscidea représente la première diversification de la branche des Ligiamorpha, c'est-à-dire la divergence comme groupes frères d'une part du groupe primitif des Diplocheta et d'autre part de la branche dans laquelle se sont diversifiés les 3 sections Microcheta, Synocheta et Crinocheta. Nous nommons cette branche Orthogonopoda, considérant l'introduction d'un terme nouveau justifiée et opérationnellement utile (Dupuis, 1979) parce qu'il s'agit d'un monophylum bien défini qui marque un niveau nettement supérieur par rapport aux Tylomorpha et aux

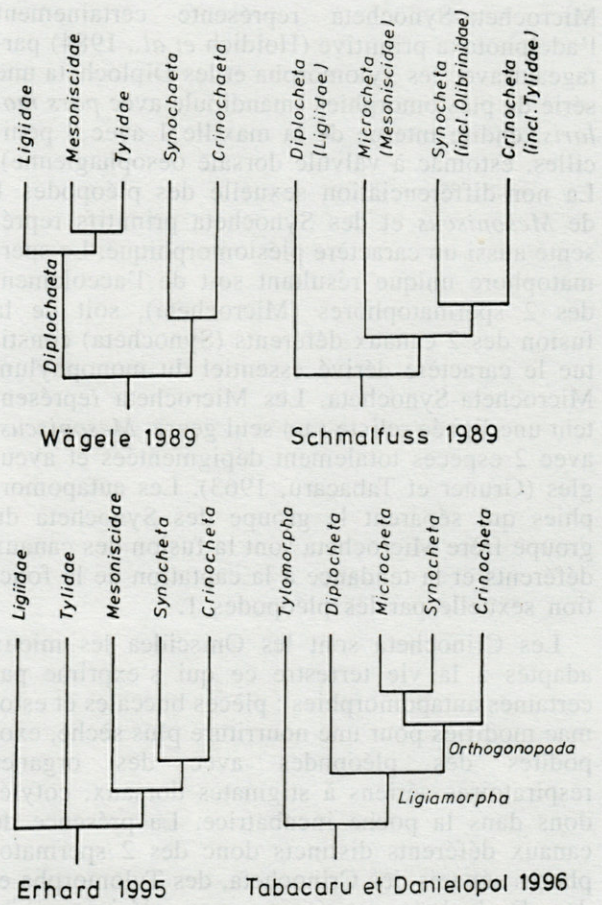

Fig. 1. – Phylogénie des Oniscidea d'après Wägele 1989, Schmalfuss 1989, Erhard 1995, et Tabacaru et Danielopol 1996.

Diplocheta. Les Diplocheta (Ligiidae) ont le plus grand nombre de plésiomorphies parmi les Oniscidea. Par leurs caractères (excepté la fusion des plaques coxales avec les péréionites), ils semblent être très proches de l'ancêtre commun des Oniscidea. Nous n'avons détecté qu'une seule apomorphie : la tendance à l'apparition, de manière originale, d'une différenciation sexuelle du premier pléopode. Les Ligiidae sont bien adaptés à un mode de vie semi-terrestre (Carefoot et Taylor, 1995) vivant soit au bord de la mer (Ligiinae), soit dans des endroits très humides (Ligidiinae). Les Orthogonopoda sont définis surtout par la conformation de l'organe copulateur (endopodite du pléopode 2 du mâle) et par la réunion des apophyses génitales.

Nous considérons comme la dernière dichotomie essentielle dans la phylogenèse des Oniscidea celle qui marque la diversification des Orthogonopoda, c'est-à-dire l'apparition d'une part de la branche qui a donné naissance aux groupes frères Microcheta-Synocheta et d'autre part de la branche des Crinocheta, groupe le plus évolué des Oniscidea. Dans cette dichotomie l'ensemble

Microcheta-Synocheta représente certainement l'adelphotaxa primitive (Holdich *et al.*, 1984) partageant avec les Tylomorpha et les Diplocheta une série de plésiomorphies (mandibule avec *pars molaris*, endite interne de la maxille 1 avec 3 penicilles, estomac à valvule dorsale oesophagienne). La non-différenciation sexuelle des pléopodes 1 de *Mesoniscus* et des Synocheta primitifs représente aussi un caractère plésiomorphique. Le spermatophore unique résultant soit de l'accolement des 2 spermatophores (Microcheta), soit de la fusion des 2 canaux déférents (Synocheta) constitue le caractère dérivé essentiel du monophylum Microcheta-Synocheta. Les Microcheta représentent une lignée relicte : un seul genre, *Mesoniscus*, avec 2 espèces totalement dépigmentées et aveugles (Gruner et Tabacaru, 1963). Les autapomorphies qui séparent le groupe des Synocheta du groupe frère Microcheta sont la fusion des canaux déférents et la tendance à la captation de la fonction sexuelle par les pléopodes 1.

Les Crinocheta sont les Oniscidea les mieux adaptés à la vie terrestre ce qui s'exprime par certaines autapomorphies : pièces buccales et estomac modifiés pour une nourriture plus sèche, exopodites des pléopodes avec des organes respiratoires aériens à stigmates dorsaux, cotylédons dans la poche incubatrice. La présence de canaux déférents distincts donc des 2 spermatophores séparés des Crinocheta, des Tylomorpha et des Diplocheta représente une plésiomorphie, mais la coaptation très poussée entre l'apophyse génitale et les endopodites 1 constitue la structure la plus efficace pour le transfert des spermatophores des Oniscidea.

L'étude cladistique réalisée nous permet de proposer la classification suivante pour les Isopodes terrestres :

Sous-ordre des Oniscidea Latreille, 1829
Infra-ordre des Tylomorpha Vandel, 1943
Famille des Tylidae
Infra-ordre des Ligiamorpha Vandel, 1943
Super-section des Diplocheta Vandel, 1957
Famille des Ligiidae
Super-section des Orthogonopoda Tabacaru et Danielopol, 1996
« Groupe Monospermophora »
Section des Microcheta Schmalfuss, 1989
Famille des Mesoniscidae
Section des Synocheta Legrand, 1946
6 familles
« Groupe Dispermophora »
Section des Crinocheta Legrand, 1946
26 familles

REMERCIEMENTS – Nous sommes très reconnaissants aux personnes qui nous ont aidé à réaliser ce travail ou qui ont discuté avec nous ce sujet : N. Coineau (Banyuls), H. Dalens (Toulouse), F. Ferrara (Florence), J. Gruber et V. Stagl (Vienne). Les séjours de I.T. en Autriche (Vienne et Mondsee) ont été effectués dans le cadre des échanges culturels entre l'Académie Autrichienne et l'Académie Roumaine.

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Reçu le 6 mai 1996 ; received May 6, 1996
Accepté le 28 mai 1996 ; accepted May 28, 1996.

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Reçu le 6 mai 1996 ; received May 6, 1996
Accepté le 28 mai 1996 ; accepted May 28, 1996.

VIE MILIEU, 1996, 46 (2) : 183-184

THE THEORY AND METHODOLOGY OF PHYLOGENETIC SYSTEMATICS IS STILL EVOLVING : A REPLY TO WILSON

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CLADISTICS
GROUNDPATTERN
PHYLOGENETIC SYSTEMATICS

ABSTRACT. – This short reply to Wilson's critique of an earlier paper by Wägele stresses that several contemporary cladists are not aware of the importance of character analysis, especially of the estimation of probability of homology and of reconstruction of groundpatterns of OTUs. The principle of parsimony should not be applied only to the comparison of tree lengths.

When Hennig first described his discoveries (Hennig 1950), namely the principles of systematics that can be derived from the theory of evolution, personal computers were not invented, collections of DNA sequences were not available, and there was no need to discuss the relevance of "unrooted trees" or the "consistency index", for example. Hennig was not a cladist in the contemporary sense. Nonetheless he was without doubt a scientist, and his method deserves to be named a scientific method, even though he worked without computers. The analysis coined by Wilson (this volume) as "Wägele's idiosyncratic method" is nothing else but Hennig's phylogenetic systematics, as used by many contemporary zoologists. I would be proud had I really discovered it. To use complex morphological characters for a cladistic analysis, Mayr and Ashlock (1991 : 212) for example recommend the following steps : 1) determination of probability of homology, 2) evaluation of character state polarity, 3) search for branches or sister-group relationships supported by apomorphies, and 4) preference for the tree topology with the smallest number of changes in character states. Of course, I have no objection against this procedure. Claus Nielsen (1995), using **supraspecific taxa** ("phyla") as OTUs, stresses that the first step is the identification of monophyletic taxa, implying that non-monophyletic groups can not be used as OTUs. He then writes (p. 7) : "The next step is the determination of ancestral characters of the phylum, and this has in some cases... made it necessary to make cladistic analyses of single phyla". In other words, he reconstructs character states in **groundpatterns** prior to inferrence of relationships among the phyla (for the descending reconstruction of groundpatterns see e.g. Sudhaus & Rehfeld 1992). Again, this obviously is not Wägele's invention.

There is not enough printing space to discuss Wilson's paper in detail. With strong language, he uses several citations from Wägele (1994) in wrong context, often misunderstanding or distorting my arguments, to show what he wants Wägele to ignore or to think. I only can recommend to read the original version (Wägele 1994) or my more general contribution in this volume. I do not have to explain, for example, why a character can be at the same time a synapomorphy and an autapomorphy, depending on the level of comparison (see e.g. Ax 1987, p. 145). More interesting is the search for the main differences in the theoretical principles. One of these is that I recommend to represent a supraspecific taxon, which is intended to be used as OTU, by its **groundpattern** (hypothetical characters of the stem species). For obvious reasons, I would refuse to use characters of single species (e.g. of *Homo sapiens* and *Rattus norvegicus*) as representative characters of the Mammalia. The search for groundpattern characters or character states is an important element of a phylogenetic analysis and therefore a central subject of many publications (e.g. Bitsch 1994, Boxshall *et al.* 1984, Ehlers 1995, Kukalová-Peck 1992, Sandeman & Scholtz 1995, Walossek 1993, etc.). The reconstruction of groundpatterns is in itself a parsimony analysis, the taxon, whose groundpattern is reconstructed, must be shown to be monophyletic. Wilson suggests that this analysis is useless and circular, which is not true : monophyly is based on apomorphies (implying also outgroup comparisons), not on complete groundpatterns, and, character analysis is **independent of tree construction**, when informative characters are used (Wägele, this volume). Interestingly, he also needs *a-priori* assumptions of monophyly (Brusca & Wilson 1991), e.g. for all supraspecific taxa of his data matrix, and he does

not discuss why for example the taxon "Mysidacea" is supposed to be a monophylum.

An important difference between the cladistic approach of the type defended by Wilson (and other contemporary cladists) and the Hennigian method is that estimation of **probability of homology**, and the intimate linkage between probability of homology of apomorphies and **probability of monophyly**, are not recognized by many cladists. This implies that the criterion of parsimony is only applied to character state distributions on tree topologies, not to character analysis (see Wägele, this volume). One of my arguments is, that tree lengths alone are of little relevance when data sets differ in their data quality. Furthermore, comparison of tree lengths is not the only method available to test different hypotheses of relationship (see e.g. Wiley 1981, p. 110-111).

My article (1994) should not be understood as a rejection of any use of computer software or as an attack against parsimony. This was not the intention : the point is that the best software will not produce acceptable results when the data are not informative or when assumptions are erroneous – the same problem exists in statistical analyses. And, this is in my opinion self-evident, an analysis is not unscientific only because computers were not used...

Phylogenetic systematics is still evolving and we are living through a phase of intense radiation of methods. The future will show, which concepts will survive. The differences existing between the methods used by some cladists (as defended by Wilson) and some hennigian morphologists are not so great as it seems at first sight. The first group should not ignore the importance of probability of homology and of groundpatterns and be aware of the pitfalls of the method, the second should be encouraged to use available software like PAUP to search for alternative hypotheses. The result would be a wider use of the principle of parsimony. Discussions as the present one will hopefully help to identify the basic, universal principles of systematics.

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VIE MILIEU, 1996, 46 (2) : 185

COMMENTS ON WÄGELE'S REPLY

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I have referred to Wägele's (1994) method as "idiosyncratic" because it is not Hennig's (1966) method. Hennig (1966) did not use groundpatterns in his phylogenetic system, and even suggested (p. 10) that bauplan research, which is similar to Wägele's groundpatterns, is essentially typological. Hennig (1966), moreover, did not provide a heuristic method for dealing with conflicting characters (homoplasy) using maximum parsimony.These features of empirical cladistics, which came after Hennig's work (see reviews of Felsenstein, 1982, and Edwards, 1996), are largely ignored by "neohennigian" phylogenetists. Wägele's method for estimating phylogenetic trees, which I find to be ineffective and unparsimonious, involves inferring *ad hoc* groundpatterns from presumed monophyletic groups and then assembling these groundpatterns, building block style, into more inclusive groundpatterns. Wägele (above) does not address this central criticism directly.

Wägele (above) misses the significance of my discussion of synapomorphy vs. autapomorphy, which meant to illuminate the mechanics of his method. Of course, a character state may be either, *depending on the analytical universe*. Empirical cladistic methods do not change the terminal taxon number during tree estimation, so a character state cannot change from presumptive synapomorphy to autapomorphy. In Wägele's method, the synapomorphic state can coalesce into an autapomorphy, as a result of his building groundpatterns from groundpatterns. Empirical cladistics is clear about this distinction : if you change the number of terminals, you have a different analysis because the relationships of the characters are also changed. As mentioned above, the changing set of terminal taxa in Wägele's method allows him to ignore global parsimony.

Wägele's reply suggests that empirical cladists do not recognise the linkage between the "probability of homology" and the "probability of monophyly". I'm certain that the average cladist is familiar the underlying theory associated with the terms "monophyly" and "homology". Wägele's references to "probability" and "data quality", however, imply *ad hoc* weighting algorithms, where monophyly and homology become confounded, such as in his dubious DNA alignment procedures (Wägele, 1995; Wägele and Stanjek, 1995). Wägele also suggests that tree lengths may not be relevant, while at the same time espousing the use of parsimony in character analysis. Clearly Wägele is not interested in parsimony.

Finally, a critical evaluation of Wägele (1994) can determine whether his ideas have been distorted or used out of context. Further discussion here is not essential.

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VIE MILIEU, 1996, 46 (2) : 186-188

ANALYSES D'OUVRAGES

BOOK REVIEWS

Actes de la 4e Conférence Internationale des Polychètes. Mémoires du Muséum National d'Histoire Naturelle Tome 162 (Zoologie) ; Editions du Muséum, Paris Déc. 1994, J.C. Dauvin, L. Laubier et D.J. Reish ed., 65 communications, 104 résumés, 642 p.

Cet ouvrage constitue les actes de la conférence tenue à Angers du 27 juillet au 1er août 1992 et organisée principalement par P. Gillet, Directeur du Laboratoire d'Ecologie Animale de l'Université Catholique de l'Ouest. Cette localisation voulait rappeler le souvenir de Pierre Fauvel qui a consacré une large partie de sa vie aux Polychètes. Les 65 communications, numérotées, se répartissent dans les disciplines suivantes : cytophysiologie, développement et reproduction (7), génétique et morphologie (8), phylogénie et taxonomie (19), écologie et biogéographie (29), aquaculture et valorisation (2). Les notes de systématique sont dominantes et l'on ne compte pas moins de 8 articles (n° 16, 19, 20, 24, 25, 29, 32 et 33) rapportant la création de nouveaux genres ou de nouvelles espèces. L'originalité la plus marquante réside dans une session réservée à la culture et à la valorisation (n° 64 et 65). Les études faunistiques localisées géographiquement sont aussi très nombreuses : (n° 22, 27, 28, 29, 38, 43, 46, 48, 51, 53, 58, 60 et 61) ; elles permettent d'aborder la diversité spécifique, même si cette diversité n'est pas traitée en tant que telle.

Cet ouvrage doit être replacé dans la série des actes des précédentes conférences. Sydney[1] (1983, 36 communications publiées), Copenhague[2] (1986, 67 contributions publiées) enfin Long Beach[3] (1989, 40 articles).

La fabrication et la présentation de cet ouvrage sont particulièrement soignées. La relecture a été très attentive et le nombre d'erreurs typographiques négligeable. Les trois rédacteurs doivent être chaleureusement félicités. Je persiste cependant à penser que, contrairement à ce que suggère le titre des actes, le groupe des Polychètes est dans une position phylétique ne permettant pas encore de les observer « en conférence ». Au-delà de ce point d'humour et du clair succès éditorial qui confirme le choix de la publication d'accueil des actes et le bien fondé de la tenue de la Conférence d'Angers, quelques réflexions méritent d'être ajoutées.

C'est quasi exclusivement la phase adulte qui fait l'objet des études de ces Actes. La morphologie, la génétique, la taxonomie, la phylogénie, l'écologie, la biogéographie s'appuient exclusivement sur cette étape du cycle de vie ; seulement 4 notes intégrent un stade larvaire (n° 40, 42, 55, 59). De ce point de vue la communauté mondiale des polychaetologues est en retard par rapport à celle traitant d'autres groupes en particulier les Echinodermes. Si, quelle que soit la discipline, les grands traits du cycle de vie sont négligés, la question restera incomplètement traitée. Ainsi la dynamique des espèces marines, leur capacité de colonisation (*cf.* n° 50) ne peuvent être comprises sans l'intégration de la dispersion larvaire. De même la compréhension de la diversité spécifique devrait s'appuyer sur les relations d'amensalisme ou de facilitation au moment de la fixation.

Au cours d'une telle réunion chaque spécialiste d'une discipline donnée constate toujours le faible nombre de communications consacrées à sa propre discipline et peut regretter les conférences « transversales » traitant de son thème de prédilection sur des groupes zoologiques variés. En fait les conférences focalisées sur les groupes zoologiques ont l'avantage de permettre de retrouver l'unité de l'organisme et l'expression de disciplines nouvelles que le spécialiste peut avec intérêt intégrer dans le contexte familial ou générique qu'il connait parfaitement.

Cet ouvrage est à recommander pour tenter de déchiffrer l'évolution des études relatives à un groupe zoologique ; aussi pour se tenir informé rapidement sur les nouvelles classifications et les familles récemment révisées. De ce point de vue cet ouvrage et les différents « proceedings » précédemment signalés devraient être utilisés par les non spécialistes chargés d'expertises faunistiques, ayant souvent à leur disposition la faune de Fauvel (parue en 1927) largement dépassée et exprimant la tendance de l'auteur au rassemblement. Il faut par conséquent se réjouir que certains travaux s'interrogent sur la réalité des espèces cosmopolites (41), démontrent l'utilisation possible en systématique des rares structures dures rencontrées chez les Polychètes (31), prennent en compte les conditions de variabilité de certains caractères au cours de l'ontogenèse (39, 59) et s'intéressent aux conditions de vie (46, 47, 48) en développant l'observation d'animaux vivants.

Cet ouvrage de base destiné à toutes les étapes de la recherche, doit être présent dans toutes les bibliothèques et les centres de recherche.

Michel BHAUD

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[1] P.A. Hutchings, ed., Proceedings of the First International Polychaete Conference. Published by the Linnean Society of New South Wales (December 1984).

[2] M.E. Petersen & J.B. Kirkegaard, eds. Proceedings of the 2nd International Polychaete Conference. *Ophelia* suppl. **5** : 1-723. (July 1986).

[3] D.J. Reish, ed. Proceedings of the third International Polychaete Conference. *Bull. Mar. Sc.* **48** (2) : 177-596 (March 1991).

FOREY P.L., C.J. HUMPHRIES, I.J. KITCHING, R.W. SCOTLAND, D.J. SIEBERT & D.M. WILLIAMS. 1992. Cladistics. A practical course in systematics. The Systematic Association n° 10, Oxford Science Publications, Clarendon Press, oxford.191 p., Hardback, £ 30.

Much ink has been spilt over cladistics and much ink will spill again over it. However cladistics is presently the most generally accepted method, inevitable by any student interested in the reconstruction of the evolutionary history of a vegetal or animal group, or in the classification of the components of such a group. In fact the purpose is the same when the requested classification is a natural classification, in which each subgroup is a group of species descending from the same ancestor and including all the descendants of this ancestor (= a monophyletic group of species). Finally the systematics aiming at the recognition of natural groups (monophyletic groups) and their relationships, is necessarily a phylogenetic systematics. Hennig is generally considered as the Father of the Phylogenetic systematics, since the publication in german language, of it's fundamental book about half a century ago (1950), exposing the basal principles of a phylogenetical analysis. Most english speaking authors discovered the interest of the Hennigian method some 15 years later, when Hennig principles were published in english (1966). The method leads to the construction of a phylogenetic tree, including a common ancestral stem and a number of branching finally giving as much lines as terminal taxa. From this characteristic pattern is derived the term «cladistics» now often used for naming the method. The seventies and eighties were the period of a wide spreading of the method. In all countries cladograms appear dealing with all groups of plants or animals. In the same time the development of personnal computers and computer programs results in the appearance of a number of parsimony programs usable in phylogeny and gradually cladistics tends to become a method of automatic calculation for the construction of the shortest tree (= the most parsimonious tree). Parsimony which was one of the Hennig principles among others tends to become the dominating principle for most modern cladists. This evolution of cladistics cannot develop without some passionate debates. However since the nineties, cladistics is widely accepted in its modern form and is more and more teached in universities and high schools, and 3 books published last years are worth retaining particulary the attention of students and researchers : the first one, published in US is «The compleat cladist» (1991); thereafter «Cladistics» was published by the British Systematic Association in 1992 and finally «Reconstruction Phylogénétique : Concepts et méthodes» was published in 1993 in France. The first book is mainly a simple course including many exercises for students; the third is a more important volume, in french language dealing with concepts and present debates. The second one is certainly, in english, an excellent handbook – the best one from my point of view – to be used by anyone looking for an initiation to the cladistic methodology or to any advanced biologist planning to teach cladistics.

This book written in a clear and simple style, is easily readable even for a french student. Produced by the collaboration of 6 British authors who have the experience of teaching taxonomy and systematics in the frame of an intense workshop on cladistics managed by the Systematic Association.

The book includes a general introduction followed by 10 chapters, the titles of which give a good idea of their content :

1. The cladistic theory (origin, basic concepts and definitions, comparison with other methods used in taxonomy). 2. The character coding (dealing with different kind of characters, usable for a phylogenetic analysis and the influence of character properties on the tree structure). 3. The determination of character polarity (with methods allowing to clear up the direction of evolutionary changes in character states). 4. The tree-building techniques (including the different types of parsimony criteria and algorithms usable to find the more parsimonious trees). 5. The different kind of trees (including the measure of confidence in a tree, the consensus trees, the alternatives to parsimony, the character weighting and the resolution of character conflicts). 6. The theory of DNA analysis. 7. The methods of DNA analysis. 8. Fossils and cladistic analysis. 9. Cladistics and biogeography. 10. Formal classifications, dealing with the implications of cladistics on taxonomy and classifications of animal Kingdom. The book ends with an important list of references (329) and an index of many terms and concepts.

No doubt that this book provides an up to date account of informations on the philosophy and mainly on the methods of modern cladistics, presented in a very pleasant style, even for a reader from a no english-speaking country. A must in any biology laboratory library.

C. BOUTIN

P. DARLU, P. TASSY, 1993. Reconstruction phylogénétique. Conceps et méthodes. Collection Biologie théorique n° 7, Masson, Paris, 245 p., broché, 16x24.

Après avoir écrit «L'arbre à remonter le temps» (1991), Pascal Tassy s'associe ici à Pierre Darlu pour publier un ouvrage pédagogique consacré aux concepts et aux méthodes de la reconstruction phylogénétique, discipline des sciences de l'évolution actuellement en plein développement. Fruit de l'expérience des deux auteurs dans ce domaine, tant dans le champ de la recherche que dans celui de l'enseignement universitaire et de la formation permanente du CNRS, ce livre de synthèse a pour objectif de présenter un panorama didactique de l'ensemble des méthodes et propose une initiation à la pratique phylogénétique ; les auteurs fournissent également des informations sur les principes et les concepts sur lesquels repose chaque méthode de sorte que le choix de l'une ou l'autre pratique se trouve grandement facilité.

Une introduction historique retrace tout d'abord le passage de la généalogie, intuitive, depuis Lamarck et Haeckel, à la phylogénie actuelle, formalisée, et pose les définitions «majeures» : arbre, concept de ressemblance, caractères et taxons. Le corps du livre développe les méthodes et la pratique et occupe plus de 190 pages réparties en 5 chapitres : la méthode cladistique (chapitres IV, V et VI), les méthodes phénétiques (chapitre VII) et les méthodes probabilistes (chapitre VIII).

Le chapitre IV expose les principes et la pratique de la méthode cladistique, fondés par Hennig : apomorphie-plésiomorphie, cladogramme-arbre phylogénétique, ancêtres, homologie, principe de parcimonie, congruence, critères d'identification du sens de transformation des caractères, polarisation et construction cladistique sont très clairement expliqués. Puis viennent les procédures de parcimonie (chap. V) liées aux logiciels de phylogénie : recherche de l'arbre le plus court (modèles, algorithmes, longueur de l'arbre), codage-optimisation et pondération des caractères ; enracinement de l'arbre, mesures de l'homoplasie, invariants. Une discussion terminant ce chapitre sur le thème « l'évolution est-elle parcimonieuse » évoque les controverses à ce sujet. La méthode de compatibilité fait l'objet du chapitre VI.

Dans les méthodes phénétiques (chapitre VII), basées sur la similitude globale, sont envisagés successivement les notions de similitude et de distance, leurs indices, les différents types de distances ainsi que les méthodes agglomératives, d'ajustement et de parcimonie. Enfin, le chapitre VIII traite des méthodes probabilistes rarement abordées de manière sysnthétique, avec notamment le principe du maximum de vraisemblance.

Toutes ces méthodes sont abondamment illustrées d'exemples concrets à l'aide de données d'ordre morphologique et moléculaire. Une discussion soulignant les particularités, les performances et les limites de chaque méthode termine chaque chapitre. Les auteurs font part également des vives controverses qui animent les débats entre partisans de l'une ou l'autre méthode. 238 références et un index complètent ce remarquable livre.

P. Darlu et P. Tassy concluent leur ouvrage en rappelant les mérites et les différences entre les méthodes de la reconstruction phylogénétique. Ils insistent sur l'importance de la première étape de cette pratique phylogénétique : l'identification de caractères pertinents. Ils montrent également qu'il est inconcevable de retracer l'histoire évolutive d'un groupe animal ou végétal en l'absence d'une reconstruction phylogénétique qui est essentielle à « la compréhension des mécanismes évolutifs qui ont conduit à la diversité ».

Ce livre, unique en son genre par son aspect synthétique, comble un vide dans la littérature scientifique traitant de systématique et d'évolution, les références d'ordre phylogénétique étant très nombreuses, mais le plus souvent dispersées dans des périodiques, d'accès relativement difficile et parfois assez hermétiques. Ici, l'information fournie est claire et facilement compréhensible, même pour les non initiés. Destiné aux étudiants de 2^{e} et 3^{e} cycles de biologie évolutive, ce livre très complet est indispensable dans toute bibliothèque universitaire, la phylogénie étant maintenant enseignée à l'Université. Il peut être également très utile aux enseignants. Il s'adresse aussi à tous les systématiciens zoologistes, botanistes ou paléontologues, ainsi qu'aux écologistes et aux chercheurs non systématiciens mais intéressés par l'évolution.

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Directeur gérant de la publication : A. GUILLE

Printed in France *Dépôt légal 2e trimestre 1996* *Commission paritaire n° 22217*

Imprimerie Louis-Jean, 05002 GAP cedex — Dépôt légal 508 — Juin 1996

INSTRUCTIONS AUX AUTEURS

TEXTE

Les manuscrits, dactylographiés en double interligne sur le recto seulement des feuilles numérotées (ne pas excéder 20 pages) sont présentés en trois jeux complets, sous leur forme définitive.

Le titre du manuscrit doit être le plus court possible; il est suivi du prénom et du nom de l'auteur (ou de chacun des auteurs) ainsi que de l'adresse (ou des adresses) du Laboratoire dans lequel a été effectué le travail.

Chaque manuscrit comportera :

— un résumé en français de 15 lignes maximum figurant en début d'article, suivi de sa traduction en anglais,
— des mots clés français et anglais (6 au maximum) permettant un traitement rapide par les revues analytiques,
— un titre abrégé pour haut de page (60 signes et espaces au plus),
— la traduction anglaise du titre de l'article,
— une liste hors-texte des légendes des illustrations et leur traduction en anglais,
— une liste hors-texte des légendes des tableaux numérotés en chiffres romains et traduites en anglais.

Les noms scientifiques (genres, espèces, sous-espèces) figurent en italiques ou soulignés d'un seul trait.

Les références bibliographiques des auteurs cités dans le texte sont regroupées à la fin du manuscrit dans l'ordre alphabétique des noms d'auteurs; elles doivent être conformes aux modèles suivants :

GRIFFITHS C.L. and J.A. KING 1979. Some relationships between size, food availability and energy balance in the Ribbed Mussel *Aulacomya ater. Mar. Biol.* **51** (2) : 141-150.

EAGLE R.A. and P.A. HARDIMAN 1977. Some observations on the relative Abundance of species in a benthic community. *In* Biology of Benthic Organisms. Edited by B.F. Keegan, P.O. Ceidigh and P.J.S. Boaden, Pergamon Press, Oxford-New York, 197-208.

Le titre des périodiques doit être abrégé d'après les règles internationales (World list of Scientific Periodicals).

Les notes infrapaginales et les remerciements seront aussi brefs que possible.

ILLUSTRATIONS

Les figures au trait doivent être exécutées à l'encre de chine sur papier calque assez fort, bristol, carte à gratter, papier millimétré bleu. Il est exigé des lettres et chiffres « transfert » par caractères autocollants pour le lettrage et la numérotation, dont la taille tient compte de la réduction à supporter. Les figures sont regroupées au maximum en planches dont la justification pleine page est 17 × 24,35 cm une fois réduites (penser à retrancher la légende de ces dimensions); largeur d'une colonne : 8,1 cm. Méthode des « rectangles homologues » pour la réduction : tracer les diagonales d'un rectangle de 17/24,35 cm, les prolonger; tout rectangle admettant ces prolongements comme diagonales correspondra à la justification après réduction. Indiquer le numéro d'ordre des figures en chiffres arabes et le nom de l'auteur au crayon bleu au recto ou au dos. Ne pas inscrire de légende sur les illustrations.

Regrouper les similis (photographies, lavis...) en planches. Employer une échelle graphique qui sera réduite avec la figure, et un lettrage par transfert. Tableaux et planches similis sont numérotés de I à N en chiffres romains. Limiter le nombre des tableaux et ne retenir que ceux qui sont indispensables à la compréhension du travail.

La revue publie gratuitement 2 planches au trait pleine page et 1 seule planche en simili; les illustrations supplémentaires ou en couleurs sont facturées aux auteurs.

ÉPREUVES ET TIRÉS À PART

Un jeu d'épreuves accompagné du manuscrit est envoyé à l'auteur qui doit retourner l'ensemble après correction et indication de la place des illustrations dans le texte, dans un délai maximum de 15 jours.

Les tirages à part, facturés directement par l'imprimeur, doivent être commandés dès réception de l'imprimé spécial joint aux épreuves.

INSTRUCTIONS TO AUTHORS

TEXT

The manuscript should by typed double-spaced on one side of white paper, format A4, pages numbered (max, 20 pp), and sent in definitive form, in triplicate, to the editor.

The title of the paper should be as concise as possible; it is followed by the first and second name of the author(s) and address of the laboratory at which the work was done. Each manuscript should include :

— a french summary of 15 lines max., followed by the english translation,
— key words in french and english (6 max.) allowing treatment by abstracting journals,
— short version of title (60 signs and spaces max.),
— english translation of the full title,
— a separate list of figure legends in english and french,
— a separate list of numbered tables with their legends in english and scientific names (genera, species, sub-species) should be written in italics or underlined once.

References of papers cited in the text should be listed at the end of the manuscript in alphabetical order, according to the following models :

GRIFFITHS C.L. and J.A. KING, 1979. Some relationships between size, food availability and energy balance in the Ribbed Mussel *Aulacomya ater. Mar. Biol.*, **51** (2) : 141-150.

EAGLE R.A. and P.A. HARDIMAN, 1977. Some observations on the relative abundance of species in a benthic community. In Biology of Benthic Organisms. Edited by B.F. Keegan, P.O. Ceidigh and P.J.S. Boaden, Pergamon Press, Oxford-New York, 197-208.

The title of a journal must be abbreviated according to the rules set by the World list of Scientific Periodicals.

Footnotes and acknowledgments should be as brief as possible.

ILLUSTRATIONS

Line drawings should be prepared with India ink on heavy tracing paper, bristol board, white drawing-cardboard or graph paper (blue grid). Letters and numbers on figures should be large enough to be easily readable after reduction; use letter transfer equipment. As far as possible, figures should be grouped in plates of 17 × 24.35 cm final size (generally the explanations are included in this frame); the width of a single column is 8.1 cm. Prepare figures using the "homologous rectangles" rule; indicate the number of the figure and the author's name with blue pencil on the back of the figure. Do not write explanations on the figure.

Photographs and half-tone drawings must always be grouped as plates. Scale bars are reduced with the figures. Number plates and tables in roman numbers on the back. Limit total number of tables to an absolute minimum of items indispensable for clear presentation.

The journal publishes free of charge two plates with line drawings and one plate of half-tone figures per article. Additional illustrations and colour plates are charged to the author(s).

GALLEY-PROOFS AND REPRINTS

One set of galley-proofs is sent with the manuscript to the author(s); both proofs and manuscript must be returned to the editor with indications on indispensable corrections and insertion of figures within two weeks.

Reprints can be ordered by using the form enclosed with the galley-proofs.

VIE ET MILIEU, 1996, 46 (2)

Life & Environment

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